THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 55, Nos. 4 and 5, pp. 123-173 August 30, 1993

No. 4. Studies of the Phylogeny and Classification of Long-Tongued Bees (Hymenoptera: Apoidea)

ARTURO ROIG-ALSINA AND CHARLES D. MICHENER

TABLE OF CONTENTS

No. 5. Phylogenetic Relationships of the Exomalopsini and Ancylini (Hymenoptera: Apidae)

FERNANDO A. SILVEIRA

TABLE OF CONTENTS

Studies of the Phylogeny and Classification of Long-Tongued Bees (Hymenoptera: Apoidea)[1]

ARTURO ROIG-ALSINA[2,3] AND CHARLES D. MICHENER[2]

ABSTRACT

Phylogenetic analyses of long-tongued bees were made using up to 82 taxa, 131 adult characters, and 77 larval characters. Only two families of long-tongued bees are recognized, Megachilidae and Apidae. The Pararhophitini and Fideliini form a subfamily, Fideliinae, of Megachilidae. The subfamilies of Apidae recognized are Nomadinae, Xylocopinae, and Apinae. The tribes Isepeolini, Osirini, and Protepeolini are part of the Apinae, not part of the Nomadinae. *Protepeolus* is a junior synonym of *Leiopodus*. The tribes Euglossini, Bombini, Apini, and Meliponini form a distinctive clade arising from within the subfamily Apinae. The Ctenoplectridae is reduced to tribal status within the Apinae. The Exomalopsini of authors is dismembered, forming the tribes Exomalopsini and Tapinotaspini, and the genus *Ancyloscelis* joining the Emphorini as a subtribe. *Eucerinoda* is included in its own subtribe in the Eucerini and the Ancylini are tentatively separate from but close to the Eucerini. New family-group names (tribal and subtribal) proposed are Hexepeolini, Brachynomadini, Tapinotaspini, and Ancyloscelina.

INTRODUCTION

Despite many studies, the classification and phylogeny of bees has never reached a stage at which most authors could agree on one classification and one probable phylogeny. Intuitive processes have led to diverse systems rather than one system. The problem is particularly acute among the long-tongued (hereafter L-T) bees (defined below), the higher taxa of which seem less differentiated than the commonly accepted families (or subfamilies) of short-tongued (S-T) bees. We therefore selected the L-T bees for cladistic study to see if more satisfying results could be obtained.

The L-T bees include the forms often placed in the families Anthophoridae (including Nomadinae and Xylocopinae), Apidae, Fideliidae and the genus *Pararhophites*, and Megachilidae; as discussed below, the family Ctenoplectridae should also be included.

The expressions L-T and S-T are in many ways inappropriate (Michener and Greenberg, 1980; Laroca et al., 1989), for there are L-T bees with short glossae and S-T bees with long glossae. The L-T bees constitute a monophyletic group ordinarily characterized by having the first two segments of the labial palpi elongate and flattened, forming with the galeae a sheath around the long glossa that is involved in the nectar imbibing process. Palpal segments 3 and 4 are small, directed laterally, and not flattened; occasionally they are absent. The monophyly of the L-T bees is further indicated by the other characters on Cladograms 1 and 2 that show L-T bees as the sister group of the Melittidae.

For some time it has been known that among parasitic Allodapini there exist species obviously related to the L-T nonparasitic allodapines but without long flat basal segments of the labial palpi and with the glossa relatively short. This trend reaches its extreme in the South African parasitic genus *Eucondylops* (Michener, 1970). The parasitic allodapines are mostly not known to visit flowers; they must feed in the nests of their host bees, other allodapines. Thus they do not need equipment for extracting nectar from flowers, and appear to have lost it. Likewise, as emphasized by Silveira (in press), the genus *Ancyla*, which visits shallow-flowered Apiaceae (Popov, 1949), has no long flat segments of the labial palpi, and yet it seems to be a close relative of *Tarsalia*, an obvious L-T bee (see Silveira, 1993). Warncke (1979) separated *Ancyla* and *Tarsalia* only subgenerically. Finally, *Ctenoplectra*, often given familial status because of its combination of characteristics of L-T bees with labial palpi of S-T bees (Michener and Greenberg, 1980), clearly is a member of the L-T bee clade (see Results); it probably lost the palpal characteristics of that clade. It follows, then, that our study includes members of the L-T bee clade, whether or not they actually have the long, flattened segments of the labial palpi. Of the three taxa listed above, however, only *Ctenoplectra* was included in the cladistic analysis; the others are too rare to dismember for detailed study and moreover, their relationships to obvious L-T bees are clear (*Eucondylops* to *Allodapula*, *Ancyla* to *Tarsalia*).

In addition to characters of adults, on which earlier classifications have been based, we have considered larval characters; we examine phylogenies based upon adults, upon larvae, and upon the two stages together. In reality, partly

---

[1] CONTRIBUTION NUMBER 3081 FROM THE DEPARTMENT OF ENTOMOLOGY, UNIVERSITY OF KANSAS, LAWRENCE.

[2] DEPARTMENT OF ENTOMOLOGY AND SNOW ENTOMOLOGICAL MUSEUM, SNOW HALL, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045-2119, USA.

[3] PRESENT ADDRESS: MUSEO ARGENTINO DE CIENCIAS NATURALES "BERNARDINO RIVADAVIA," BUENOS AIRES, ARGENTINA.

because they are still known only from a limited number of taxa, the larvae contributed relatively little to our conclusions.

The following abbreviations are used throughout this work:

L-T	long-tongued
S-T	short-tongued
T1, T2, etc.	first, second, etc. metasomal terga
S1, S2, etc.	first, second, etc. metasomal sterna

In the phylogenetic analyses, L = tree length, T = number of trees, ci = consistency index, and ri = retention index.

ACKNOWLEDGMENTS

Our work was greatly facilitated by National Science Foundation grant BSR 87-16817 (C. D. Michener, principal investigator). Preparation of the cladograms in form for publication was largely by Douglas Yanega. For editorial and bibliographic help, we thank Virginia Ashlock. A. R.-A.'s work in Lawrence was possible thanks to the Organization of American States and the Consejo Nacional de Investigaciones Cientificas y Tecnicas, Republica de Argentina.

We appreciate the opportunity to discuss methodological and other problems with B. Alexander, J. S. Ashe, and S. Reyes of the University of Kansas.

HISTORY OF THE CLASSIFICATION OF LONG-TONGUED BEES

This section is by no means an exhaustive treatment of the history of apoid classification, or classification of L-T bees. We limit ourselves to several classifications to illustrate the diversity of opinions, and to some more recent works that have a direct bearing on our work. We also limit ourselves, in this section, to adult characters since characters of immature stages have not played a major role in bee classification.

In his great work on British bees, Kirby (1802) distinguished L-T from S-T bees, using a generic name for each, *Apis* and *Melitta* respectively. In the same year Latreille (1802) recognized the same two groups as families, the Apiariae and Andrenetae. Subsequent authors such as Smith (1853), Cresson (1887) and Warncke (1977) recognized the same two families, Apidae and Andrenidae.

There were, however, divergent opinions. Lepeletier (1836, 1841) and Schmiedeknecht (1882) classified bees on the basis of habits: solitary, social, and parasitic. There were L-T bees included in each of these three categories. Many subsequent classifications followed this system, placing parasitic bees in separate taxa from the nonparasitic ones. Ashmead (1899) also put all bees that he knew to be parasitic (even *Psithyrus*) in separate families, but these were placed among his families of nonparasitic bees. Tkalců (1972, 1974) revived the idea of separate clades for all parasitic bees (cleptoparasites as well as social parasites like *Psithyrus*), suggesting that they arose from non-pollen-collecting ancestors of the pollen-collecting taxa. This would imply that there were different wasp ancestors for the various major groups of parasitic bees and therefore for groups of other bees as well. To us there is strong evidence for monophyly of all bees (Brothers, 1975), as well as of the L-T bees (Michener and Greenberg, 1980).

Another classification that intermixed L-T and S-T bees was that of Robertson (1904). His was a thoughtful classification, but based almost exclusively on the fauna of a limited region (southern Illinois). It divided bees into two groups of families, those with and those without pygidial plates. Had Robertson studied any of the majority of Colletinae in the world (for example, *Leioproctus*) that have pygidial plates, he would have recognized his error. It is now clear that the plate is an ancestral character that has been lost independently among various lineages of bees as well as wasps, but Robertson's classification was widely accepted for several decades.

We turn now more strictly to the L-T bees. Schenck (1859, 1869) transferred *Ceratina* from the parasitic bees, where it had been placed by Lepeletier (1841), to the Anthophoridae. (He also included the S-T genera *Melitturga* and *Systropha* in the Anthophoridae.) Even Börner (1919) still placed *Ceratina* among the parasitic bees in the Nomadidae. Schenck also separated the parasitic megachilids from the parasitic anthophorids, but did not place either with its nonparasitic relatives. It is relevant to our study that Schenck placed melittids between the S-T families (he called them subfamilies but used the -idae ending) and the L-T families. Thomson (1872) placed most of the parasites in taxa (tribes) with their nonparasitic relatives but associated the melittids (S-T) with *Ceratina* and *Anthophora* in one tribe.

Robertson (1904) was the first to clearly recognize such groups as the Eucerini and Emphorini; he called them families.

Michener (1944) recognized the Lithurginae as quite different from the Megachilinae in spite of similar appearance. He also recognized numerous tribes of Nomadinae, separate from the parasitic Anthophorinae such as the tribe Melectini. He assembled the Melittidae, our principal outgroup for the study of L-T bees, although it had earlier been dispersed in various ways and sometimes associated with rophitine or panurgine genera, and he included *Ctenoplectra* in the Melittidae. He placed the Fideliinae and the Anthophorinae in the Apidae, *Pararhophites* being in the subfamily Anthophorinae. Minor subsequent modifications were summarized by the classification used in Michener (1979). Anthophoridae was unfortunately recognized there as a family separate from Apidae.

Šustera (1958) proposed a classification in many ways not too different from those of Michener, but with the Nomadinae divided. The Nomadini, Ammobatini and Pasitini were in the Andrenidae, an S-T family, while the Epeolini, Epeoloidini, and other parasitic anthophorines remained in the Anthophoridae, an L-T family.

Warncke (1977) gave a quite different classification, as noted above, using the two families Apidae and Andrenidae. Like some other authors, he recognized the similarity of Melittidae (an S-T family) to L-T bees, and indeed he placed them (as a subfamily) in the Apidae. *Pararhophites* was included in the Melittinae. Other features that seem strange are inclusion of *Exomalopsis* and *Fidelia* in the Ceratininae, and of *Manuelia* and *Xylocopa* with *Ancyla* in one group of Anthophorinae.

Rozen (1977), after studying larvae of Fideliinae, transferred the subfamily to the Megachilidae. McGinley and Rozen (1987) supported the above placement of Fideliinae and Rozen in the same paper placed *Pararhophites* near the Fideliinae in the Megachilidae. These placements are strongly supported by the present study.

Michener and Greenberg (1980) supported the placement of Melittidae as derived from other S-T bees, as indicated by Michener in 1944. They considered Melittidae as the sister group to Ctenoplectridae and the L-T bees together, and separated Ctenoplectridae from the Melittidae as a family of S-T bees with features of L-T bees, and the sister group to the L-T bees. We show that this placement is incorrect in the Phylogenetic Analyses, below.

Sakagami and Michener (1987) proposed the tribe Manueliini in the Xylocopinae, and indicated that the Xylocopinae and the apine clade (meaning Apini, Bombini, Euglossini, and Meliponini) are sister groups. This viewpoint is not supported by the present study.

From this brief and incomplete historical review, the lack of consensus throughout the history of bee classification is clear. Disagreement as to taxonomic rank is of minor importance; recent authors place bees in one, two, or up to eleven families. The interesting disagreements concern inferred phylogenetic relationships, which can be indicated, if desired, within a classification regardless of the taxonomic rank.

SELECTION OF TAXA

The 82 taxa used in our analysis of adults were selected to represent as nearly as possible all subfamilies and tribes of L-T bees and of the outgroup, the Melittidae (Table 1). Where there is considerable diversity within a tribe or subfamily, more than one genus was often selected, particularly if relations within the taxon are poorly understood, as, for example, in the groups that were included in the Exomalopsini (*sensu* Michener and Moure, 1957). Two subgenera of certain genera were included. We believe that the representatives selected provide a good survey of the diversity among L-T bees, although there are only 82 species representing perhaps 10,000 species of L-T bees.

For each genus or subgenus included in the study, a particular species was selected for detailed examination, primarily on the basis of abundance of material. It is characters of such species that are the bases for the phylogenetic discussion and analysis; the species are listed in Table 1. For the sake of brevity we often refer to characters of a genus, tribe, etc., but in reality we mean, of the selected exemplars. Of course we believe that in most cases the characters listed for a species are those of its genus and its tribe, etc., and we have examined the external characters of species other than the exemplars. In some cases we know of interspecific variation in some of the characters used in our study. An alternative approach would have been to analyze generic characters, tribal characters, etc. This would have involved recording characters of many species in order to determine which are the generic characters and would have required exclusion of various characters because most species would not have been available for dismemberment and study of the internal skeletal characters that are involved in our study. Of course if phylogenies were available for each genus, tribe, etc., one would be in a better position to select characters of each for analysis in a broader study. We believe that the use of exemplars is more practical and probably better considering the present state of the study of apoid phylogeny.

When family, subfamily, or tribal names are used, reference is to the taxa as understood in the classification proposed in the section on Classificatory Results.

Unfortunately, because of lack of material for dissection, there remain a few taxa of questionable phylogenetic position that could not be examined in full detail and that are excluded from the analysis. One of these is the genus *Ancyla*. It is perhaps closely related to *Tarsalia* (Silveira, 1993 and in press) and the two were included in the same genus by Warncke (1979). *Ancyla* is interesting principally because of the reduced labial palpi and rather short glossa, as indicated in the Introduction. Another is *Townsendiella;* the Townsendiellini are not represented in our study although the position of this taxon is reasonably well known (see Roig-Alsina, 1991). It would also have been desirable to include *Epeoloides*, presumably a divergent member of the Osirini, sometimes placed in a tribe Epeoloidini. *Dioxys* could well have been included; it is a divergent member of the Anthidiini.

The larval study is largely based on the data recorded by McGinley (1981, Appendix 1). To his table of data we added character states for *Pararhophites* (from McGinley and Rozen, 1987) and *Paratetrapedia* (from Rozen and Michener, 1988), since these are genera of great interest in bee systematics. Fortunately their characters were reported in such a way that the data could easily be extracted and coded to correspond to McGinley's Appendix 1.

The species in the larval study are those listed by McGinley (1981, Table 1), plus *Pararhophites orobinus* (Morawitz) and *Paratetrapedia swainsonae* (Cockerell).

SELECTION OF CHARACTERS

Contrary to the recent practice of one of us (CDM), we use the word *character* for a feature that varies among taxa, and the expression *character state* for the condition of that character in a particular taxon. Thus "head color" is a character, and "head red" indicates a character state. This is contrary to taxonomists' usual usage but is in agreement with both pheneticists' and cladists' usage and has become well established. The resultant double meaning for *character*,

Table 1. List of Taxa Used as Adult Exemplars

Taxa are listed in the same sequence as in the matrix of adult characters (Table 2). The last nine taxa are S-T bees not included in the matrix.

Eremapis parvula Ogloblin
Teratognatha modesta Ogloblin
Isomalopsis niveata (Friese)
Exomalopsis jenseni Friese
Tapinotaspis (Tapinotaspoides) tucumana (Vachal)
Tapinotaspis (Tapinorhina) caerulea (Friese)
Paratetrapedia (Arhysoceble) melampoda (Moure)
P. (Paratetrapedia) sp. (Chamela, Mex.)
Monoeca lanei (Moure)
Caenonomada bruneri Ashmead
Ancyloscelis apiformis (Fabricius)
Melitoma segmentaria (Fabricius)
Diadasia pereyrae (Holmberg)
Diadasina distincta (Holmberg)
Ptilothrix tricolor (Friese)
Tetrapedia sp. (La Rioja, Arg.)
Coelioxoides waltheriae Ducke
Tarsalia ancyliformis Popov
Eucerinoda gayi (Spinola)
Canephorula apiformis (Friese)
Eucera chrysopyga Pérez
Melissodes agilis Cresson
Svastra obliqua (Say)
Peponapis fervens (Smith)
Anthophora paranensis Holmberg
Habropoda laboriosa (Fabricius); *H. pallida* (Timberlake)
Deltoptila elefas (Friese)
Centris tricolor Friese
Epicharis elegans Smith
Xeromelecta californica (Cresson)
Zacosmia maculata (Cresson)
Thyreus ramosa (Lepeletier)
Ericrocis lata (Cresson)
Mesonychium jenseni (Friese)
Mesoplia rufipes (Perty)
Rhathymus bicolor Lepeletier
Parepeolus aterrimus (Friese)
Ecclitodes stuardi (Ruiz)
Osiris variegatus Smith
Leiopodus lacertinus Smith
Isepeolus vachali Jörgensen
Melectoides triseriatus (Friese)
Neolarra verbesinae (Cockerell)
Caenoprosopis crabronina Holmberg
Oreopasites arizonica Linsley
Triepeolus distinctus (Cresson)
Epeolus compactus Cresson
Rhogepeolus bigibbosus Moure
Holcopasites calliopsidis (Linsley)
Brachynomada sp. (Argentina)
Kelita sp. (Argentina)
Nomada (Pachynomada) utahensis Moalif
N. (Centrias) sp. (Kansas)
Biastes brevicornis (Panzer)
Hexepeolus rhodogyne Linsley and Michener
Manuelia gayi (Spinola)
Xylocopa virginica (Linnaeus)
Ceratina calcarata Robertson; *C. rupestris* Holmberg
Macrogalea candida (Smith)
Braunsapis facialis (Gerstaecker)
Bombus pennsylvanicus (De Geer)
Apis mellifera Linnaeus
Melipona fulva Lepeletier
Partamona cupira (Smith)
Euglossa cordata (Linnaeus)
Eufriesea violacea (Blanchard)
Pararhophites orobinus (Morawitz)
Neofidelia profuga Moure and Michener
Parafidelia friesei Brauns
Lithurge apicalis Cresson
Trachusa (Heteranthidium) bequaerti (Schwarz)
Anthidium porterae Cockerell
Hoplitis albifrons (Kirby)
Osmia lignaria Say
Megachile petulans Cresson
Coelioxys octodentata Say
Ctenoplectra fuscipes (Friese)
Macropis steironematis Robertson
Melitta leporina (Panzer)
Dasypoda panzeri Spinola
Hesperapis ilicifoliae (Cockerell); *H. carinata* Stevens
Meganomia gigas Michener

S-T Bees

Andrena erythrogaster Ashmead
Protandrena mexicanorum Cockerell
Leioproctus delahozi Toro
Colletes inaequalis Say
Caupolicana ruficollis Friese
Dufourea marginata (Cresson)
Nomia triangulifera Vachal
Halictus rubicundus (Christ)
Augochlora pura (Say)

sometimes meaning that which varies and sometimes the condition of a particular taxon, rarely causes confusion, and particularly in the section on classification we regularly refer, for example, to Character 30-1 instead of writing out Character 30, State (1).

Adults of all the included species (Table 1) were not only examined externally, but were treated with 10% KOH (room temperature, for a day or more), dismembered to get appropriate views of interesting structures, and examined and stored in glycerin.

Selection of characters for use in a study such as this is extremely important. We do not know the ideal way of doing so. There is an infinity of characters that might be found and used in a study of a large group such as the L-T bees. We excluded autapomorphies because they do not contribute to knowledge of intertaxon relationships. Characters that seem to be autapomorphic (i.e., are on terminal taxa) on the cladograms also appear somewhere else in the cladogram. We limited ourselves to characters for which a reasonable assumption about polarity could be made. That is, we included no character for which the plesiomorphic state for L-T bees could not be recognized with some degree of confidence by means of outgroup comparisons as described in the next section.

These practices exclude a multitude of characters that might be used in detailed analyses of smaller groups. For example, features of punctation, surface sculpture, facial proportions, distribution and color of pubescence, and details of shape of the hidden sterna and male genitalia might all be polarizable and valuable in a study of a limited taxon, a genus or perhaps a tribe. These characters, however, cannot be polarized for a large taxon like the L-T bees because they vary kaleidoscopically within both the L-T bees and the outgroups. Since it is impossible to pick out a state for such a character that is plesiomorphic relative to the rest of the states, it is not a polarizable character. The problem is identifying similarities that are homologous and determining their points of origin, things that can often be done within a genus or tribe but that become difficult for similar characters in high-ranking taxa.

With the exceptions indicated below, we included all characters that we found for which a strong hypothesis as to the plesiomorphic state could be made. Nearly all of the characters are those of the exoskeleton, but many involve internal ridges and apodemes.

A problem that arises is the possibility of biasing the selection of characters to produce a certain phylogeny or classification. To some degree this may be impossible to avoid when characters are selected by specialists in the group who have *a priori* ideas about relationships. However, by using all the characters that we found whose polarity could be determined, we hope to have largely avoided this problem. We believe that *a posteriori* searching for characters to produce a desired result is not legitimate. For example, we suspect that the Exomalopsini, which appears as a paraphyletic group in our study, is in reality monophyletic, and as noted in the section on Classificatory Results, some of our characters suggest this, as does a later study by Silveira (1993). We do not believe that it would be legitimate to search for more characters *in order to* establish monophyly of the group: one might thereby fail to find other evidence showing some taxa to have closer relatives in other groups. The proper procedure would be a more detailed study of the Exomalopsini and its relatives, again using *all* characters that can be found that are polarizable within the group of *Exomalopsis* and its relatives.

SELECTION AND CODING OF CHARACTERS OF ADULTS

The principles used in selecting characters are described above. A few characters, however, were omitted even though we know the plesiomorphic states. Among these was number of segments in the maxillary palpi, which is plesiomorphically 6, but is reduced in various taxa to 5, 4, 3, 2, and 1. The reductions are often variable within taxa, even within species, so that coding is difficult; moreover, such reductions can be seen in most higher taxa. For this reason we believed that this character would contribute little to our knowledge of phylogeny of higher taxa. Some characters that we did use in the analysis also proved to be of little value, but we did not have ready knowledge that this would be the case until the study was made.

A character that we omitted from analysis concerns the seriate disannular hairs of the glossa, which we initially coded as follows: (0) Long, divergent. (1) Minute and ordinarily convergent, invaginated inside glossal canal. (2) Absent. There are two rows of seriate hairs; see Michener and Brooks (1984). They are long and divergent in most S-T bees. Because in L-T bees they are often minute, visible only with dissection and a compound microscope, the distinction between States (1) and (2) was not verified for some taxa and the character was therefore excluded from the analyses. For our study the distinction between State (0) and the others would only have added one character to strengthen the differences between S-T bees (including Melittidae) and L-T bees, i.e., it would have added a character to Nodes 3 and 41 of Cladograms 1a, 1b and 2a, 2b. These are already strongly supported nodes. It is in the Nomadinae and similar parasites that the seriate hairs sometimes become especially small, sparse, and even absent.

Another character that was omitted from the analyses was presence or absence of the hind tibial scopa. It is lost in Megachilinae and parasitic bees. We excluded it (and did not reintroduce it) in an early attempt (before the Analyses reported here) to diminish the effect of convergence among parasitic bees.

Polarity was determined by comparison with five genera representing all three subfamilies of Melittidae (Table 1), the principal outgroup. Melittidae was selected as the closest outgroup because it shares a number of characters with L-T bees even though it is an S-T family on the bases of numerous other characters. Its position was well indicated by Michener and Greenberg (1980). Because a melittid character could be a family-level apomorphy, or because of variation among the five melittid taxa, the states of certain characters were also determined for certain species in other S-T families. Taxa of these families used are listed at the end of Table 1. The phylogeny of the S-T families has not been analyzed; we examined members of the Andrenidae, Colletidae and Halictidae relevant to all characters used in our analyses. The Halictidae appears to be derived in many features, and it was therefore principally from examination of Andrenidae and Colletidae that we determined whether polarities based on melittid character states were verified or required modification. When modification seemed appropriate, it is explained in the annotated lists of characters.

The plesiomorphic state was coded (0). For the other states, in characters with two or more other states, no assumption was made as to a phylogenetic sequence of those states; all were run as unordered. There were 37 multistate characters in our analysis of adults and 12 in the analysis of larvae. For individual characters, many of the problems concerning polarity and application of codes are explained in the lists of characters. Some characters relate to structures that are absent in certain taxa. For example, we list characters of the flabellum, a structure that is sometimes absent. In such cases, the character is coded as (?) for taxa lacking the structure. The same code is used if a structure cannot be observed, for example, because of lack of material.

ANNOTATED LIST OF ADULT CHARACTERS

1. Subantennal suture: (0) Directed toward lower margin of antennal socket, sometimes divided (Y-shaped) below socket. (1) Directed toward outer margin of socket. When the suture is Y-shaped, the outer branch is directed toward the outer margin of the socket but the lower, undivided stem is directed toward the lower margin. State (1) is characteristic of Megachilinae.

2. Anterior tentorial pit: (0) High on epistomal suture. (1) At or below middle of lateral part of epistomal suture.

3. Integument of paraocular area: (0) Not differentiated from more median part of frons. (1) Narrow area bordering eye with punctures sparser and smaller than rest of frons, paler in cleared specimens, margins sometimes diffuse. (2) Such an area broad, ovoid, with sharp limits (more distinct in female than in male). Smaller areas, in particular [e.g., State (1)], are not recognizable except in cleared specimens. At least in State (2) there is a layer of possibly glandular tissue underlying the area. Such areas are suggestive of the facial foveae of many colletid and andrenid bees. Our polarization is based on the absence of such areas in Melittidae, but such absence could be a synapomorphy of that family. Their absence also in Megachilidae [although State (1) occurs in Fideliini], Nomadinae and Xylocopinae supports the polarization

indicated above for the L-T bees and especially for the Apidae. State (2) is characteristic of *Exomalopsis*, its allies such as *Eremapis*, and also *Tapinotaspis*.

4. Paraocular carina: (0) Absent. (1) Present.

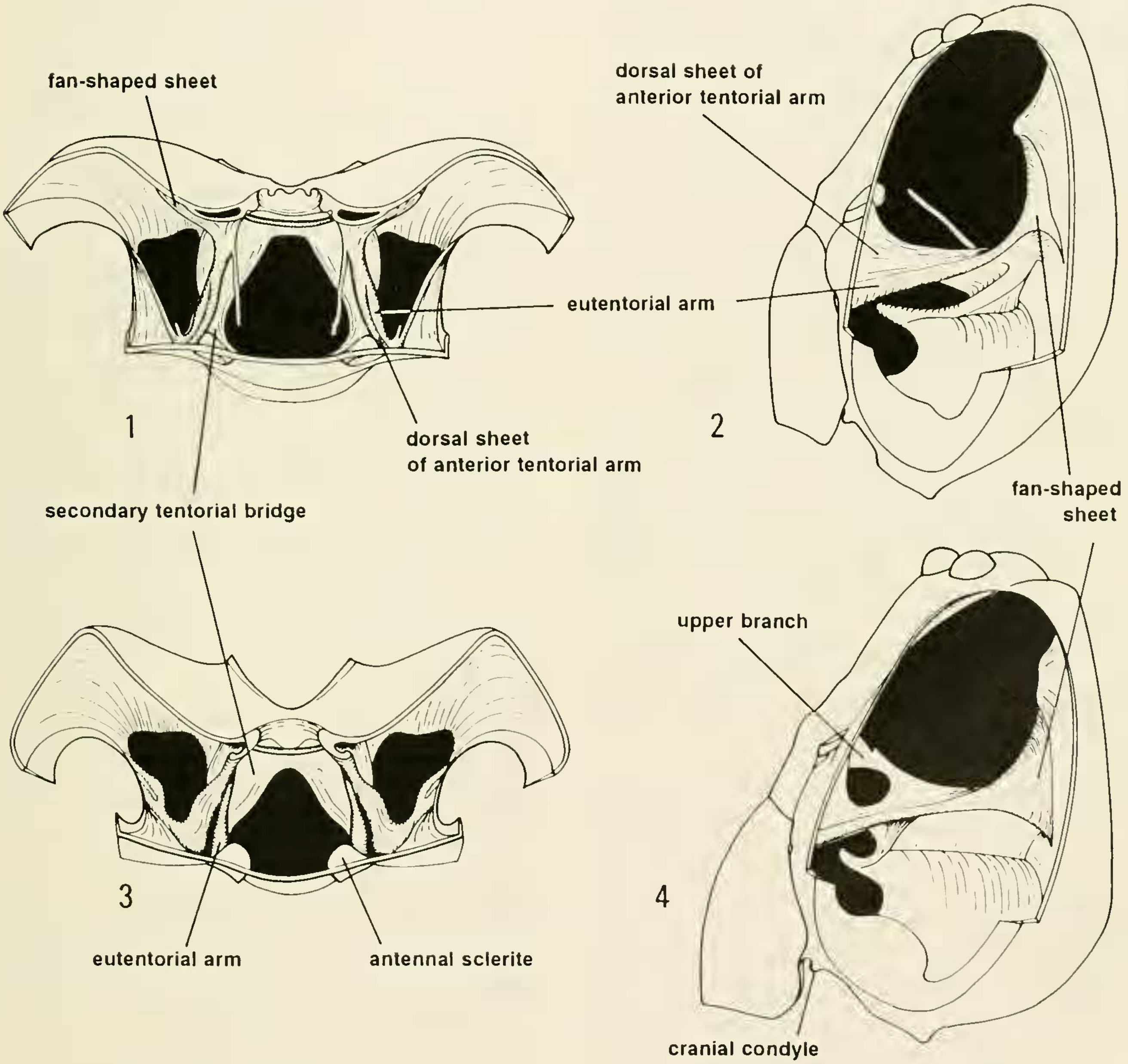
5. Condyle of anterior mandibular articulation (cranial condyle): (0) Contiguous with lateral clypeal margin. (1) Partly covered by lateral clypeal margin, which is usually elevated over condyle (Fig. 4). The melittids (except some *Hesperapis*) exhibit State (1). However, because State (0) characterizes other S-T bees, most melittids appear to be derived in this character.

6. Lateral part of lower portion of clypeus: (0) Not bent backward or only gently curved backward. (1) Strongly and abruptly bent back, so that lateral parts are at angle of 90° to 115° to median part.

7. Labrum: (0) Broader than long. (1) Longer than broad.

8. Anterior surface of labrum of female: (0) With basal polished area, sometimes elevated, clearly delimited from punctate and hairy disc. (1) Without basal polished area. *Neofidelia* has a short polished area, perhaps equivalent to that described above; it was coded (1), however.

9. Erect labral setae: (0) Not forming a U- or V-shaped row. (1) Coarse setae forming U- or V-shaped row, with midpoint (base of



Figs. 1-4. Head capsule, female; muscles and eyes removed to show tentorial structure. **1.** *Centris tricolor*, transverse section above antennal insertions, view from above. **2.** *Centris tricolor*, head sectioned along paraocular area, lateral view. **3.** *Anthidium porterae*, transverse section above antennal insertions, view from above. **4.** *Melissodes agilis*, head sectioned along paraocular area, lateral view.

U or V) near apex of labrum and lateral arms extending basad near margins of labrum. State (1) occurs in many megachilids.

10. Tuft on apical margin of labrum: (0) Absent. (1) Present. Although present in *Dasypoda*, such a tuft is absent in most S-T bees.

11. Antennal sclerite: (0) Not extending internally beyond antennifer (Figs. 6, 7). (1) Extending internally beyond antennifer (Figs. 9, 10). State (1) is characteristic of Emphorini and *Coelioxoides; Ancyloscelis* is intermediate but was coded (1) like other Emphorini.

12. Dorsal sheet of anterior tentorial arm: (0) Without a branch united with upper wall of antennal socket (Fig. 2). (1) With such a branch (Fig. 4). State (1) is characteristic of Eucerini.

13. Dorsal sheet of anterior tentorial arm: (0) Without spur reaching orbit of eye. (1) With spur reaching laterally to eye margin and indicated externally by transverse line or scar across paraocular area at level of antenna. State (1) is characteristic of Euglossini.

14. Union of anterior tentorial arm to head wall below antennal socket: (0) Reaching lower margin of antennal socket so that no triangular space is enclosed (Fig. 5). (1) Forming triangular space between dorsal sheet of tentorial arm and attachment of thickening of secondary tentorial bridge, but space small and not always recognizable externally by Y-shaped subantennal suture. (2) Space large, forming triangular subantennal area (Fig. 8) recognizable externally between arms of Y-shaped subantennal suture and lower margin of antennal socket. In *Biastes* the dorsal sheet of the anterior tentorial arm ends below the antennal socket, as does the secondary tentorial bridge; it was coded (0). In Euglossini the attachment of the tentorial arm is so modified that it is difficult to code and in *Partamona* the antennae are so close to the epistomal suture that interpretation is difficult. These were coded (?).

15. Thickening of secondary tentorial bridge: (0) Uniting to head wall at or below antennal socket (Fig. 1). (1) Merging with eutentorial arm before reaching head wall (Fig. 3).

16. Lateral expansion of internal thickening above epistomal ridge: (0) At least as wide as half width of socket diameter (Fig. 5). (1) Reduced, less than half width of socket diameter.

17. Clypeus with apical inflection: (0) Present (Figs. 5-10). (1) Reduced to narrow band.

18. Lateral carina of clypeus, along lower part of epistomal suture of male, and associated groove lateral to it: (0) Absent. (1) Present (Ehrenfeld and Rozen, 1977, Fig. 14). State (1) is found only in certain Nomadinae.

19. Epistomal ridge (internal manifestation of epistomal suture): (0) Well developed (Fig. 5). (1) Absent below tentorial pit.

20. Epistomal ridge below tentorial pit: (0) Receiving sheet from eutentorial arm, this sheet margined internally by a thickening (Figs. 6, 7). (1) Receiving such a sheet which is not margined by a thickening. (2) Without a sheet from the eutentorial arm (Figs. 5, 8-10).

21. Postoccipital pouch below foramen magnum: (0) Absent. (1) Shallow. (2) Distinct and deep (Fig. 12). This feature is variable in melittids, but is absent in other S-T bees; (0) is therefore considered plesiomorphic although most melittids were coded (2).

22. Fan-shaped posterior sheets of tentorium, sometimes represented externally by the occipital sulci: (0) Well developed (Figs. 1, 2, 4). (1) Small to absent (Fig. 3).

23. Attachment of secondary tentorial bridge to posterior wall of head (below foramen magnum): (0) Above and separate from hypostoma at upper end of proboscidial fossa, but connected to hypostoma by vertical septum usually manifest externally as vertical black line extending upward from upper end of proboscidial fossa (Fig. 11). (1) As in (0) but vertical line wider, clear, representing thicker septum. (2) Secondary bridge fused directly to hypostoma, thus eliminating vertical black line, fusion evident externally in that lines of attachment of bridge to head wall reach hypostoma at upper end of proboscidial fossa independently and separated by clear zone (Fig. 12). This character is variable in Melittidae but other S-T bees have State (0) except for *Dufourea*, which has State (2).

24. Epistomal suture below anterior tentorial pits: (0) Nearly straight or gently curved or angulate so that sides of clypeus diverge strongly. (1) Extending straight down, then abruptly angulate laterad, so that sides of upper part of clypeus are about parallel.

25. Ventral sclerite of neck: (0) Absent. (1) Present (Roig-Alsina, 1989, Fig. 4). State (1) is found only in Osirini.

26. Articulation of maxillary cardo and stipes: (0) Without small triangular sclerite (Fig. 13). (1) With small (to minute) triangular intercalary sclerite. State (1) is found only in Melittidae but is not found in other bees and appears to be a synapomorphy of that family. It therefore adds nothing to our study.

27. Maxillary stipes with basal process (Winston, 1979, Fig. 2b): (0) Not produced mesally. (1) Produced mesally, elongate. Although State (0) appears in *Apis*, State (1) is in general characteristic of L-T bees and Melittidae (Michener and Greenberg, 1980).

28. Length of stipital comb-bearing concavity: (0) Over one-fourth length of stipes. (1) One-fourth length of stipes or less, deep (Brooks, 1988, Fig. 5). State (1) is found only in Anthophorini.

29. Maxillary stipes with comb in concavity on distal posterior margin: (0) Absent. (1) Present (Fig. 14). When a comb is present it is always in a concavity. Only some Nomadinae have a concavity from which the comb was probably lost.

30. Maxillary stipes with ridge on outer surface: (0) Absent. (1) Present (Fig. 14). There is some variation in this character. For example, in *Melitta, Ctenoplectra*, and *Euglossa*, the ridge is limited to the apical half or third of the stipes. In *Ceratina* the ridge is near the posterior margin of the outer surface instead of near the middle. In *Melipona* there is an angle but no sharp ridge. Although the character is variable in Melittidae, other S-T bees are coded (0), which is therefore considered plesiomorphic.

31. Dististipital process: (0) Absent. (1) Present, curved anteriorly (Fig. 15b; Winston, 1979, Fig. 7b). State (1) is found only in Megachilinae.

32. Maxillary stipes with expansion on distal anterior margin (opposite to comb and concavity): (0) Absent. (1) Present (Fig. 14).

33. Maxillary palpus with brush of hairs on third segment: (0) Absent. (1) Present. State (1) is found only in Emphorini.

34. Maxillary galea with comb on inner surface: (0) Present (Michener, 1981, Figs. 10-13). (1) Absent. This comb is principally a character of S-T bees (including Melittidae) although *Xeromelecta* has a comb. *Deltoptila, Rhathymus*, and *Thyreus* [coded as (1)] have some hairs in this area.

35. Maxillary galea: (0) Without row of bristles. (1) With longitudinal row of bristles on anterior margin of internal surface (Fig. 15b). The row is sometimes limited to the apical third or fourth, as in *Anthophora, Deltoptila, Mesoplia*, and *Zacosmia;* these were all coded as (1).

36. Maxillary galeal blade: (0) Uniformly sclerotized or only narrowly desclerotized near apex. (1) With posterior margin broadly desclerotized almost to base (Fig. 15).

37. Membrane underlying maxillary lacinia: (0) Unsclerotized, not striate. (1) Striate, sometimes weakly sclerotized.

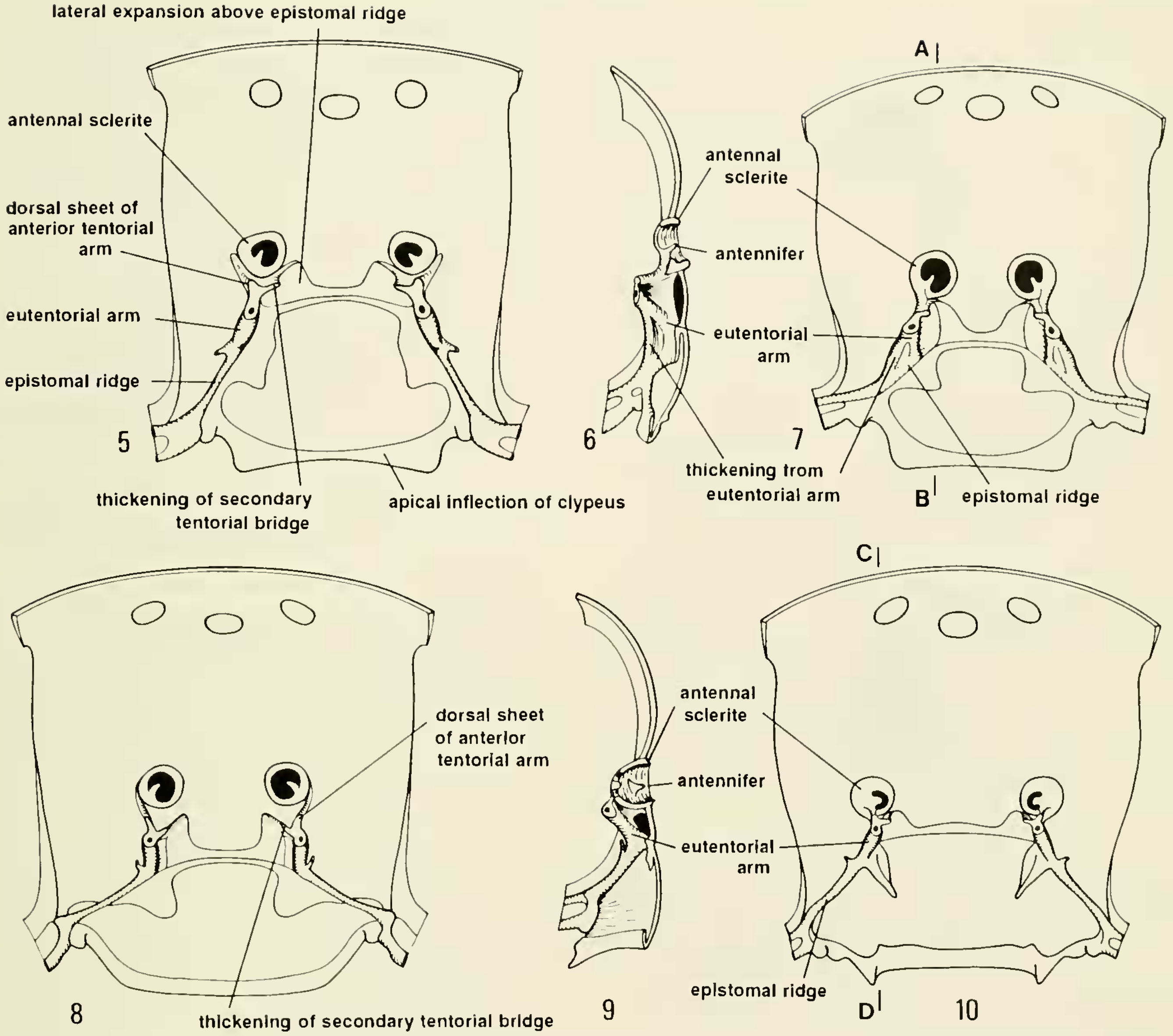
38. Maxillary lacinia: (0) Sclerotized. (1) Membranous.

39. Maxillary lacinia: (0) Rounded. (1) Elongate.

40. Stipital sclerite [terminology of Winston (1979, Fig. 2b)] of maxilla: (0) Distinct. (1) Fused to rest of stipes.

41. Galeal blade (midway between base and apex) with internal sclerotized surface: (0) As wide as external surface. (1) At most two-thirds as wide as external surface (Fig. 15b, c). (2) Three-fourths as wide as external surface or more but narrower than external surface. When the internal surface is narrower than the outer, the anterior edge of the former often appears as a dark line which is the midrib of the galea of Winston (1979).

42. Lorum: (0) Platelike, flat or bent around base of mentum (Michener, 1985, Fig. 31). (1) V-shaped with slender arms (Michener, 1985, Fig. 45). State (1) is characteristic of Melittidae and L-T bees, i.e., of all taxa in our analysis [see Michener and Greenberg (1980)]. This character therefore does not contribute to our analysis.



Figs. 5-10. Anterior wall of the head, female; heads sectioned at level of anterior mandibular articulations. 5, 7, 8, 10, posterior (internal) views; 6, 9, longitudinal sections of 7 and 10 on planes AB and CD, respectively. **5.** *Centris tricolor.* **6, 7.** *Macropis steironematis.* **8.** *Tapinotaspis tucumana.* **9, 10.** *Diadasia pereyrae.*

43. Lorum and mentum: (0) United. (1) Separated from one another.

44. Base of lorum: (0) Simple. (1) With a longitudinal fissure on each side (Plant and Paulus, 1987, Fig. 12).

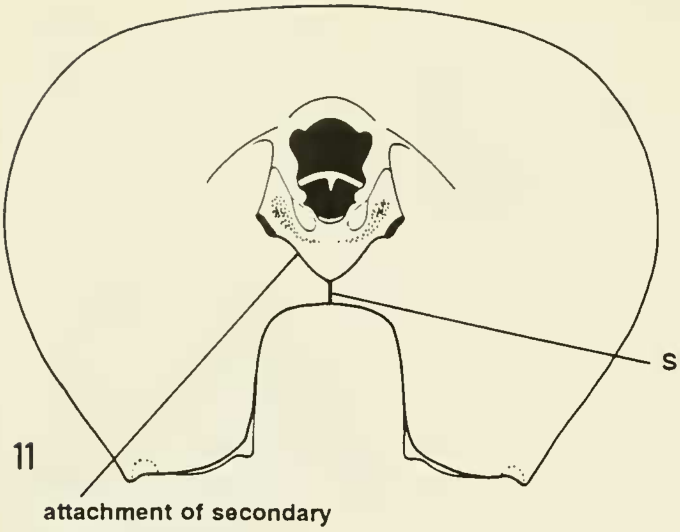
45. Base of prementum: (0) With a fragmentum isolated or partly isolated from rest of prementum (Michener, 1985, Fig. 43). (1) Without such a fragmentum. In *Bombus, Centris, Diadasina, Epicharis,* and *Ptilothrix* there is a projection from the base of the prementum; they were coded (1). For bees as a whole, lack of a fragmentum must be plesiomorphic since there is no fragmentum in most S-T bees. However, it is present in Melittidae and Andrenidae. We therefore consider presence of a fragmentum as plesiomorphic for L-T bees.

46. Subligular process of prementum (Winston, 1979, Fig. 2c): (0) Fully sclerotized and united to rest of prementum (Fig. 16). (1) Separated from rest of prementum by weak line. (2) Weakly sclerotized.

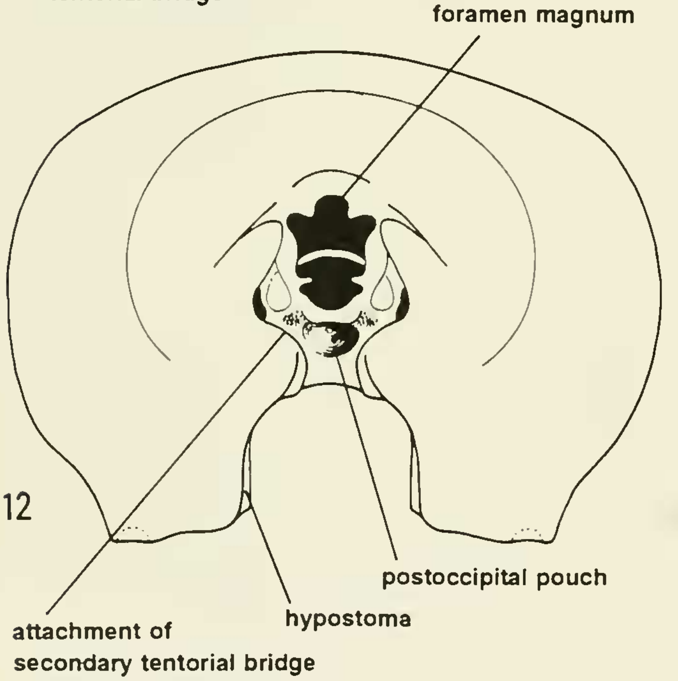
47. Small sclerite lateral to subligular process of prementum: (0) Absent. (1) Present (Fig. 16). These sclerites are quite distinct in *Leiopodus* and *Ancyloscelis* but are weakly sclerotized and difficult to see in other genera coded (1).

48. Labial palpus segments 1 and 2: (0) Not particularly flattened, similar in form and length to segments 3 and 4. (1) Greatly elongated compared to segments 3 and 4, usually flattened. State (1) is characteristic of L-T bees in general. The first palpal segment in *Lithurge* is short, similar to that of a melittid, although the second segment is long and flat. *Lithurge* was coded (0).

49. Labial palpus, base of segment 1: (0) Parallel sided. (1) Inner margin incised so that base is strongly narrowed (Fig. 16; Winston, 1979, Fig. 35).



11



12

Figs. 11, 12. Head capsule, female, posterior view. **11.** *Macropis steironematis;* S, line corresponding to internal vertical septum. **12.** *Melitoma segmentaria.*

50. First segment of labial palpus: (0) Without membranous margin (Figs. 16, 17a, b). (1) With membranous inner margin (Fig. 17c, d).

51. Disannulate surface of glossa: (0) Exposed, nearly as large as annulate surface (Michener and Brooks, 1984, Fig. 5). (1) Invaginated, annulate surface surrounding almost whole glossa (Michener and Brooks, 1984, Fig. 8). In various parasitic taxa (e.g., *Isepeolus, Leiopodus, Nomada, Triepeolus,* and *Xeromelecta*) the disannular surface is considerably exposed. It is nonetheless much smaller than the annular surface and the degree of exposure is difficult to assess. Such forms were coded as (1).

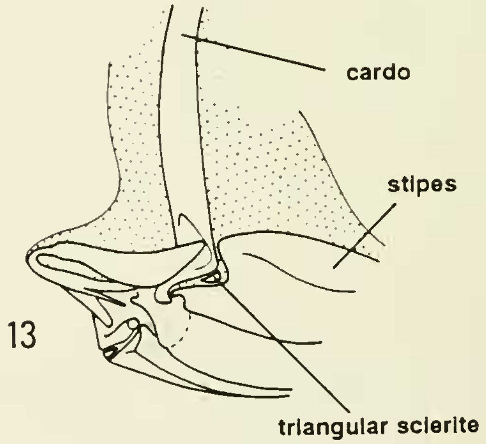
52. Glossal rod (Michener and Brooks, 1984, Fig. 9): (0) Absent. (1) Present but not enclosing bacular canal. (2) Present and partly surrounding the bacular canal (Michener and Brooks, 1984, Fig. 89). For terminology, see Michener and Brooks (1984). State (1) is found in sphecids and most S-T bees including melittids. In most Melectini and Nomadinae the rod is weakly sclerotized and thin (i.e., flat). Such forms are coded as (1), even though the rod seems to be reduced. Michener and Brooks (1984) considered the rod absent in some Nomadinae, but we found at least a stiffer strip in all whose glossae we dissected. There are all degrees of reduction, and the rod is well developed in *Caenoprosopis, Thalestria* and *Triepeolus* in the Nomadinae, as well as in other parasitic forms such as *Leiopodus* and *Isepeolus.* State (2) is rare outside the apine clade; it is not associated with heavy pigmentation in spite of the large size of the rod (see Michener and Brooks, 1984).

53. Flabellum (Michener and Brooks, 1984, Fig. 8): (0) Absent. (1) A flabellum-like structure present but not constricted at its base. (2) Present, constricted at its base. A flabellum is absent in most S-T bees including most melittids. There are all degrees of flabellar development, of which we recognize two levels, (1) and (2). Presence of a well-developed flabellum in some panurgine Andrenidae presumably shows that it can arise independently. It can also be lost, as in *Habropoda,* where its absence is an autapomorphy rather than a plesiomorphy.

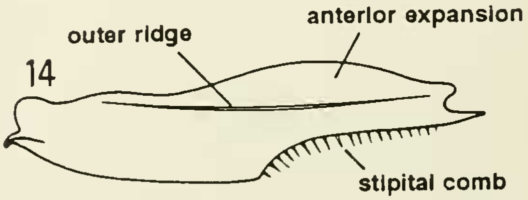
54. Posterior surface of flabellum: (0) Smooth or nearly so. (1) With a cobblestone pattern (Michener and Brooks, 1984, Fig. 94F). Except on the flabellum-like structure of *Dasyposa* (Melittidae), there is nothing among S-T bees to suggest a cobblestone pattern.

55. Annular hairs of glossa: (0) Extending to base of flabellum. (1) Separated from flabellum by a non-annulate shank (Michener and Brooks, 1984, Fig. 99B). Incompletely developed flabella are always set among the distal annular hairs, as are many fully developed flabella with basal constrictions. In a few taxa the fully developed flabellum is at the end of a largely bare shank.

56. Basiglossal sclerite (Michener and Brooks, 1984, Fig. 7): (0)

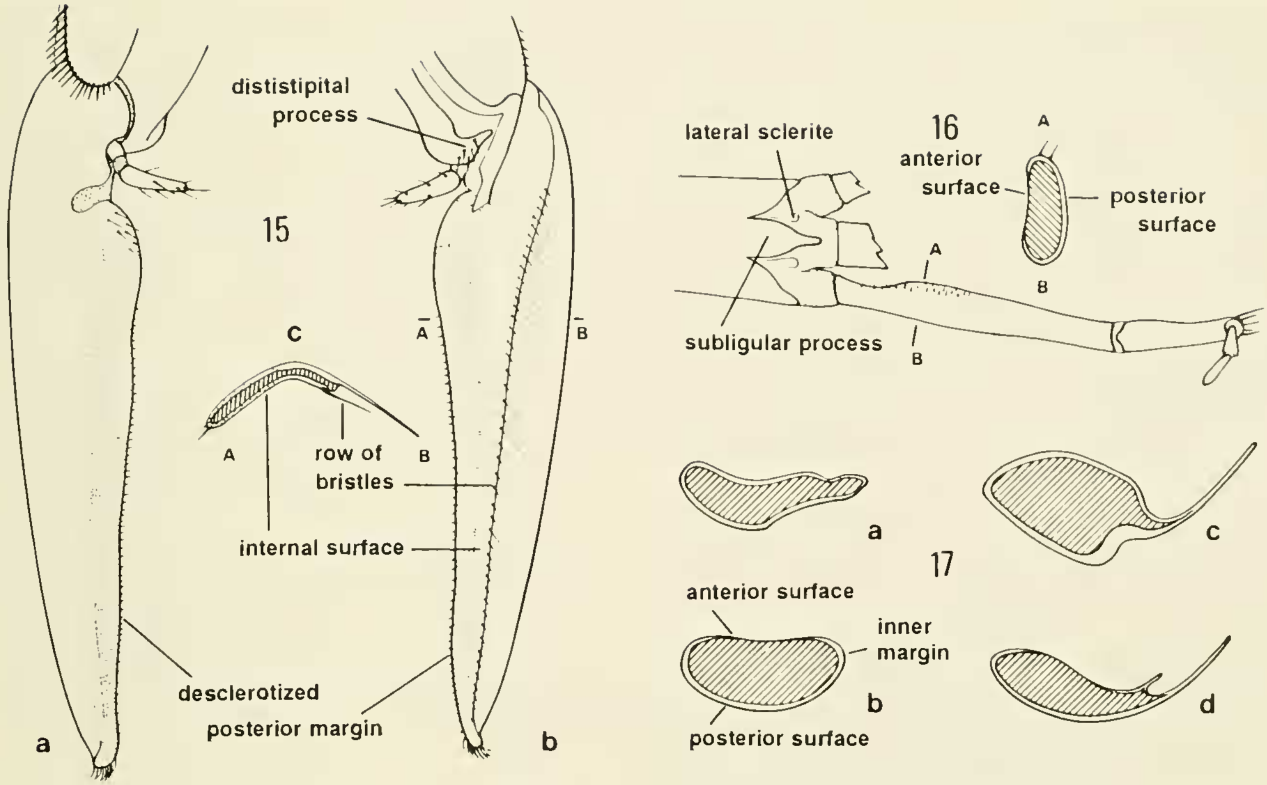


13



14

Figs. 13, 14: 13. *Macropis steironematis,* posterolateral view of portion of proboscis showing articulation of cardo, stipes and lorum. **14.** *Melitoma segmentaria,* stipes, external view.



Figs. 15-17: 15. *Anthidium porterae*, female. Maxillary galea: a, external view; b, internal view; c, cross section near basal third, at plane AB. **16.** *Tapinotaspis caerulea*, labial palpus and apex of prementum, posterior view and cross section of labial palpus near base. **17.** Cross sections of first segment of labial palpus near basal fourth: a, *Anthidium porterae;* b, *Melitoma segmentaria;* c, *Bombus pennsylvanicus;* d, *Habropoda laboriosa.*

A transverse band across base of glossa. (1) More elongate, often longer than broad (sometimes medially cleft), laterally with posterior basal process extending around side of base of glossa. S-T bees have State (0).

57. Flabellum: (0) Not divided. (1) Divided into preflabellum and postflabellum arising from preapical anterior surface of preflabellum (Michener and Brooks, 1984, Fig. 96F). State (1) is characteristic of Ericrocidini.

58. Paraglossa beyond apex of suspensorium: (0) Shorter than to 1.3 times length of suspensorium. (1) 1.5 to 2.5 times length of suspensorium. (2) Over 3 times length of suspensorium. In melittids the range is up to 1.2. State (2) is characteristic of the Eucerini.

59. Mandibular apex of female: (0) Simple or with lower tooth longer than others. (1) With lower tooth, formed from end of adductor ridge, shorter than next tooth, the mandible being tridentate with middle tooth longest (Michener and Fraser, 1978, Figs. 22, 29). State (1) is found in *Lithurge* and some Xylocopinae.

60. Mandible of female: (0) Slender, region of pollex not expanded distally (Michener and Fraser, 1978, Fig. 12). (1) With region of pollex expanded to form two to several teeth or an edentate margin above rutellum (Michener and Fraser, 1978, Figs. 34, 41). State (1) is characteristic of Megachilidae and at least some members of the apine clade.

61. Mandibular grooves and ridges on outer surface: (0) Distinct. (1) Largely absent. State (1) is found only in the Meliponini and Apini.

62. Pronotum with ventrolateral extensions: (0) Fused midventrally, usually on internal surfaces of extensions. (1) Separated midventrally (Fig. 18). This character is variable in Melittidae but colletids, andrenids, and *Dufourea* in the Halictidae show State (0).

63. Lateral carina separating exposed part of propleuron from part hidden by pronotum: (0) Present (Fig. 19). (1) Absent.

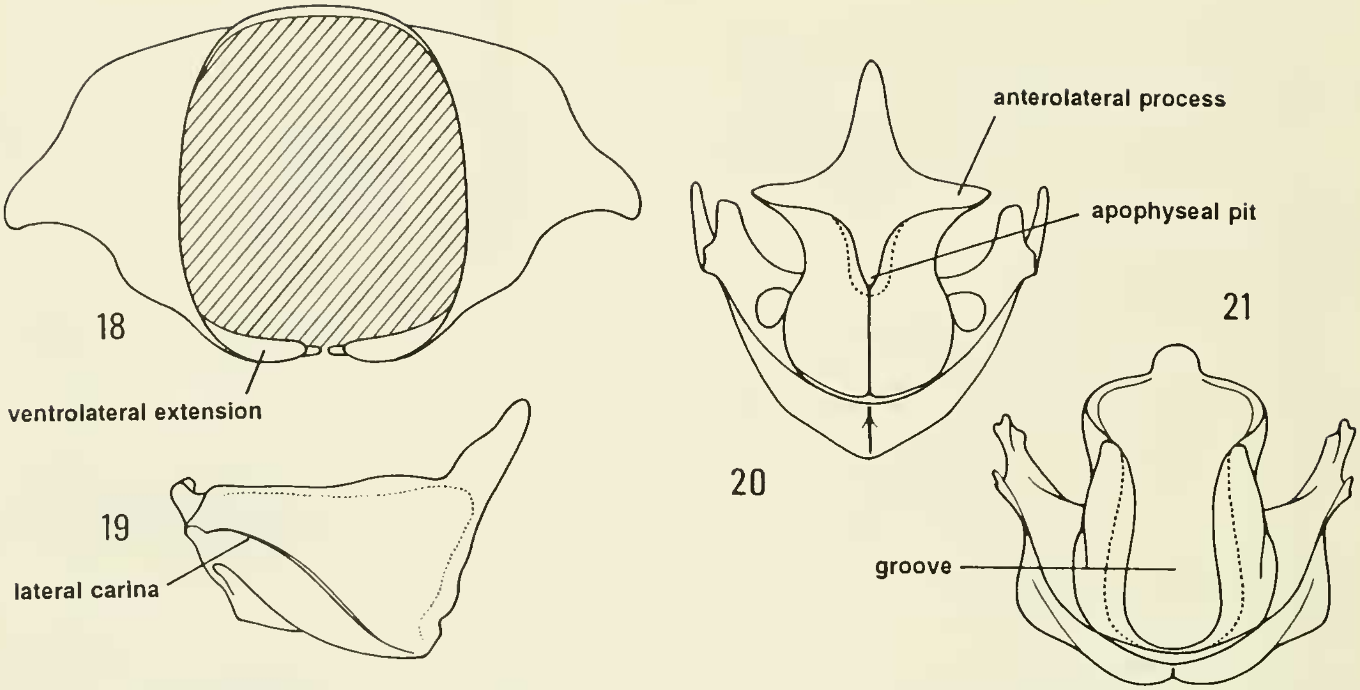
64. Apophyseal arms of prosternum: (0) Fused along median crest. (1) Separate from one another (Michener, 1944, Fig. 26). Although melittids were all coded (1), all other S-T bees show State (0). Presumably State (1) is an apomorphy for melittids and for some L-T bees.

65. Apophyseal pit of prosternum: (0) Present, near middle of prosternum (Fig. 20). (1) Expanded to posterior extremity of prosternum as broad groove (Fig. 21). (2) Absent.

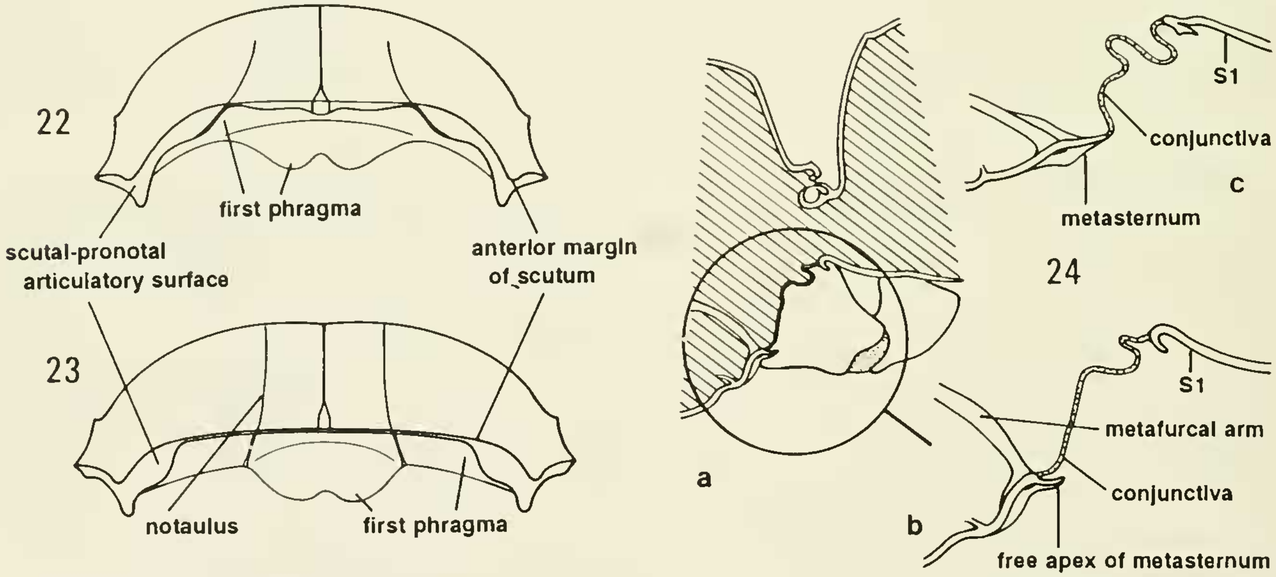
66. Prosternal shape: (0) Not or moderately constricted medially, anterolateral processes shorter and less attenuate (Fig. 20). (1) Strongly and acutely constricted in front of middle, anterolateral processes large and attenuate laterally (Prentice, 1991, Fig. 3.3). State (1) is found only in Apini and Meliponini.

67. First phragma: (0) Not bearing anterior end of internal ridge representing notaulus (Fig. 22). (1) Bearing on posterior surface anterior end of notaular ridge (Fig. 23).

68. Pre-episternal internal ridge (corresponding at least in part to external pre-episternal groove): (0) Directed anteroventrally, more or less straight, reaching down to or surpassing level of pleural scrobe. (1) Curved posteriorly toward scrobe; in this case the corresponding external groove demarks the anterior and lower margins of the swollen hypoepimeral area. (2) Short, not reaching level of scrobe, so that one cannot tell whether it is straight (0) or curved (1). (3) Absent. A long, straight ridge is present in most S-T bees, even though Melittidae exhibit State (3), presumably as a synapomorphy for the family. Presence of such a ridge is therefore considered plesiomorphic. In L-T bees, however, such a ridge is long only in *Caenoprosopis*, *Neofidelia* and *Oreopasites*,



Figs. 18-21: 18. *Melissodes agilis*, female; pronotum, anterior view. **19.** *Melitoma segmentaria*, female; propleuron, lateral view. **20.** Prosternum, female, ventral view, *Melissodes agilis*. **21.** Same, *Mesonychium jenseni*.



Figs. 22-24: 22. Scutum, female, anterior view, *Canephorula apiformis*. **23.** Same, *Melitoma segmentaria*. **24.** Articulation between mesosoma and metasoma, sagittal section; a, b, *Melissodes agilis*; c, *Paratetrapedia* sp.

and is present but only slightly surpasses the level of the scrobe in *Leiopodus* and *Isepeolus*. These taxa are so diverse that one wonders if the ridge may have arisen independently in certain cases. If so, our polarization, while correct for bees as a whole, is wrong for L-T bees. In this case, State (3), as in Melittidae, should be considered plesiomorphic.

69. Internal scrobal ridge from mesepisternal scrobe posteriorly to intersegmental suture: (0) Absent. (1) Present. Although melittids are variable in this character, other S-T bees have State (0).

70. Breadth of metapleuron at level of upper metapleural pit divided by height of metapleuron measured from lower end to apex of wing process: (0) 0.20 or more. (1) 0.19 or less. In Melittidae and other S-T bees the ratio is 0.21 to 0.30.

71. Distance between metapleural pits divided by height of metapleuron (measured as for Character 70): (0) Over 0.20. (1)

0.10 to 0.19. (2) 0.09 or less. The pits are far apart in Melittidae (0.20 to 0.35) and other S-T bees.

72. Membrane closing space behind metasternum and hind coxae and extending to base of S1: (0) Arising above free apex of metasternum on ridge between the hind coxal condyles (Fig. 24a, b). (1) Arising from apical margin of metasternum, which therefore is not free (Fig. 24c). In *Apis*, *Braunsapis*, *Ceratina*, Euglossini, and *Parafidelia* the free part of the metasternum is very short, but they are coded as (0).

73. Propodeal profile: (0) With a nearly horizontal basal zone, behind which it rather abruptly turns downward to form the declivous posterior surface. (1) With a steeply slanting or sometimes convex basal zone or entirely declivous. This character is variable in Melittidae as in some other major bee taxa, but State (0) is so prevalent among S-T bees as well as sphecoid wasps that it must be plesiomorphic.

74. Profile of metanotum (and scutellum): (0) Subhorizontal or slanting, scutellum frequently convex but also basically subhorizontal or slanting. (1) Vertical, not overhung by convex scutellum whose posterior margin is more or less vertical. (2) Vertical, strongly overhung by scutellum whose posterior margin faces more or less downward.

75. Lower extremity of metapostnotum (propodeal triangle) internally: (0) With vertical longitudinal ridge (third phragma) whose lower end is above marginal area of propodeum (Fig. 25). (1) With longitudinal ridge extending downward to marginal area of propodeum. (2) With ridge extending beyond marginal area of propodeum as acute point visible through propodeal articulating orifice when the metasoma is removed (Fig. 26), the ridge sometimes largely absent but point clearly visible. (3) Absent.

76. Hind coxal articulation: (0) Clearly above submarginal groove of propodeum-metapleuron (Fig. 25). (1) At or below level of submarginal groove (Fig. 26).

77. Articulation of propodeum with T1: (0) Forming a simple tooth at each side of articulating orifice (Figs. 25, 26). (1) Forming two teeth at each side of articulating orifice (Fig. 27). State (1) is found only in Anthophorini.

78. Conjunctiva between metasternum, hind coxae, and S1: (0) Entirely membranous. (1) With sclerotized bars near coxal margins, meeting one another or fused near posterior point of metasternum (Snodgrass, 1956, Fig. 33C). The sclerotized bars suggest a remnant of the propodeal sternum, present in many wasps, apparently lost in bees. State (1) is found only in certain members of the apine clade.

79. Metapostnotum (propodeal triangle) with hairs: (0) Absent. (1) Present and widespread. State (0) is found in most S-T bees including the Melittidae.

80. Hind trochanter with inner basal surface: (0) Angulate (Fig. 29). (1) Rounded (Fig. 28). State (0) is frequent in S-T bees.

81. Degree of isolation of bases of hind tibial spurs by sclerotized bridges around articulations of spurs: (0) None to partial (Cane's [1979] codes 0 to 2). (1) Almost complete (Cane's code 2+ for both spurs). (2) Complete, with sclerotic bridge between spur bases (Cane's code 3 for both spurs). Like melittids, other S-T bees exhibit State (0).

82. Inner margin of inner hind tibial spur of female: (0) Finely serrate to ciliate (coarsely serrate in Fideliinae). (1) Pectinate, with long, strong teeth. Many S-T bees, including melittids, exhibit State (0).

83. Outer hind tibial spur (usually inner also) of female: (0) Finely serrate or ciliate. (1) Coarsely serrate. (2) Absent.

84. Basitibial plate: (0) Present at least in female. (1) Absent.

85. Hind tibial scopa (female): (0) Absent or consisting of uniformly dispersed hairs on outer side of tibia, i.e., corbicula absent. (1) Surrounding large polished space on outer side of tibia, i.e., corbicula. State (1) is found in the apine clade and in *Canephorula* in the Eucerini.

86. Apex of inner surface of hind tibia (female): (0) Without comb of bristles. (1) With comb of bristles, i.e., the rastellum. State (1) is found in the apine clade.

87. Apex of hind tibia (female): (0) Not expanded dorsally, so that basitarsus is articulated near dorsal margin and appears to arise near middle of apex of tibia. (1) Expanded dorsally, so that basitarsus is articulated away from dorsal margin. The expansion [found only in the apine clade, except slightly present in *Ctenoplectra*, coded (1)] is perhaps an aspect of broadening the tibia for a corbicula, but does not occur in *Canephorula*.

88. Base of hind basitarsus (female): (0) Not broadened. (1) Widened to form the auricle which pushes pollen up into corbicula. State (1) occurs only in the Apini, Bombini and Euglossini. In Euglossini the structure is quite different and it may not be homologous to the auricle of Apini and Bombini.

89. Hind basitarsus (female): (0) Giving rise to second tarsomere at apex. (1) Projecting distad above articulation of second tarsomere as process without an apical brush. (2) Projecting distad as in (1) but ending in a small dense brush (penicillus). The polarity indicated above is based on State (0) in our outgroup, the Melittidae. However, many S-T bees have a penicillus. If the loss of the penicillus and process is a melittid apomorphy, then State (2) or possibly (1) would be the proper plesiomorphic condition for L-T bees.

90. Shape of hind basitarsus (female): (0) Over 3.0 times as long as wide. (1) 1.5 times as long as wide or less. (2) 1.6 to 2.9 times as long as wide, i.e., intermediate. This character is variable in Melittidae but the other S-T bees studied, except *Caupolicana*, have State (0).

91. Under surface of middle tibia of female: (0) With oblique longitudinal ridge bearing a longitudinal brush (mid tibial comb of Jander, 1976) of hairs (Fig. 30). (1) Flat, with more scattered hairs (Fig. 31). This character is variable in melittids; polarization is based on the prevalence of State (0) in other S-T bees.

92. Middle tibial spur: (0) Finely serrate or ciliate, with apex simple. (1) Coarsely serrate, with apex simple. (2) Serrate but ending in two to several large teeth or spines. State (2) is characteristic of Ericrocidini.

93. Row of stout setae on middle basitarsus (female): (0) Absent. (1) Present (Neff and Simpson, 1981, Fig. 5). State (1) is a feature of some oil-collecting bees.

94. Front basitarsal comb of female, a row of strong setae extending from apex of strigilar concavity nearly to apex of tarsomere, distal part of comb curved: (0) Absent. (1) Present (Neff and Simpson, 1981, Fig. 13). This is a feature of some oil-collecting bees. Similar combs in different positions on the basitarsus are present in *Tetrapedia* and *Paratetrapedia*. They are autapomorphies and therefore not included in the analysis.

95. Trunk of anterior tibial spur: (0) Simple. (1) With low expansion at right angles to velum, curving apically into spine of malus. (2) With strong expansion at right angles to velum, ending in strong angle or prong (Schönitzer and Renner, 1980, Fig. 19). The expansion described for State (2) is the anterior velum of Schönitzer (1986).

96. Velum of anterior tibial spur: (0) Narrow, 1.5 or more times longer than wide, usually lenticular, thus widest near middle. (1) Broad, 1.10 to 1.45 times as long as broad, quadrate. (2) About as long as broad (0.95-1.05). Although this character varies in Melittidae, the frequency of State (0) in other S-T bees justifies our polarization (see Schönitzer, 1986).

97. Anterior coxa with carina along inner margin, frequently bending laterad at base and extending partway across base of coxa: (0) Absent. (1) Present (Roig-Alsina, 1989, Fig. 4). State (1) is characteristic of Osirini.

98. Arolia: (0) Present. (1) Absent.

99. Claws of female: (0) Cleft, inner ramus sometimes a tooth. (1) Simple. Forms with the lower ramus broad, flattened, and blunt are nonetheless coded (0).

100. Number of submarginal cells in forewing: (0) Three. (1) Two. (2) None clearly defined, although faint veins often present. State (2) is characteristic of Meliponini. Although variable in Melittidae, State (0) is so common in S-T bees and in wasps that it is clearly plesiomorphic. Reduction to two cells has occurred inde-

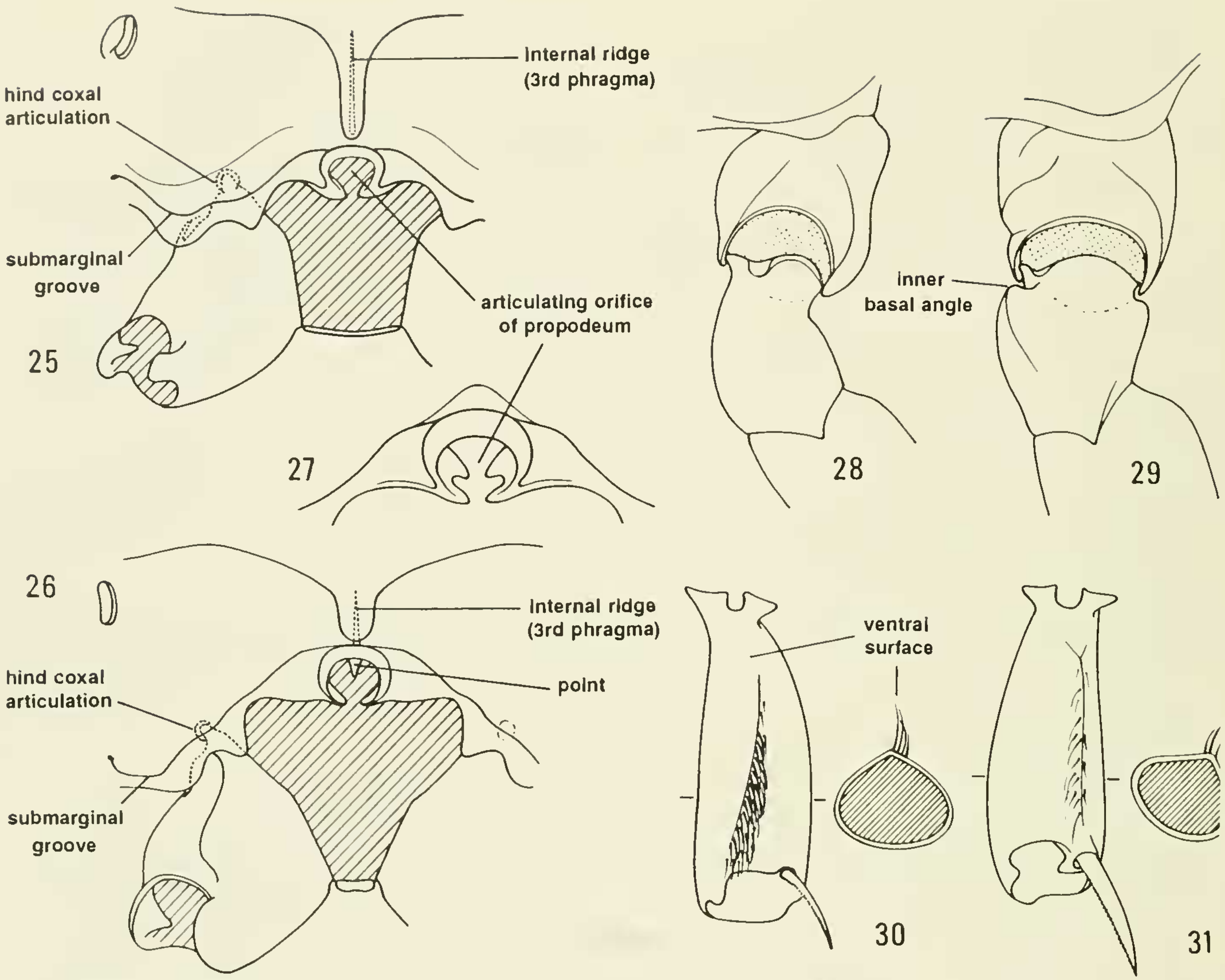


Fig. 25-31: 25. Propodeum, metapostnotum and hind coxa, posterior view, female, *Macropis steironematis*. **26.** Same, *Canephorula apiformis*. **27.** Articular region only, *Habropoda laboriosa*. **28.** Right hind coxa and trochanter, of *Anthidium porterae*, female, viewed from above. **29.** Same, of *Svastra obliqua*. **30.** Right middle tibia, of *Macropis steironematis*, female, ventral view and cross section near apical third. **31.** Same, of *Melissodes agilis*.

pendently and perhaps even by different means. In most cases it is by loss of the second transverse cubital but in some, the first transverse cubital may be lost. If this is true, of course there are two characters with identical plesiomorphic states, because loss of one vein is not homologous to loss of another.

101. Wing vestiture: (0) Hairy throughout. (1) Partly bare.

102. Length of marginal cell of forewing: (0) Equal to or longer than distance from its apex to wing tip. (1) Shorter than distance from its apex to wing tip.

103. Apex of marginal cell of forewing: (0) Pointed, on wing margin. (1) Separated from wing margin, pointed. (2) Separated from wing margin, rounded. (3) Open or closed by weak vein. State (3) is found only in Meliponini. Although variable in Melittidae, State (0) is the principal one found in that family and in other S-T bees and, being commonly associated with other plesiomorphic characters such as a large stigma, is considered plesiomorphic.

104. Stigma of forewing: (0) Longer than broad, length beyond vein r at least half as long as margin basal to vein r, margin within marginal cell convex or sometimes straight. (1) Longer than broad, length beyond vein r less than half as long as part basal to vein r, margin within marginal cell concave. (2) Small, about as long as broad to nearly absent. (3) Narrow, almost parallel-sided, as in *Apis*. State (0) is the usual condition in S-T bees; the exceptions are seemingly derived taxa like the Diphaglossinae and *Colletes* (Colletidae).

105. Jugal lobe of hind wing: (0) Long, 0.5 times length of vannal lobe (measured from wing base) or more. (1) Short, 0.26 to 0.49 times length of vannal lobe. (2) Shorter, 0.25 times length of vannal lobe or less. (3) Absent. In S-T bees the jugal lobe is long, e.g., 0.75 times length of vannal lobe or more. State (0) is therefore considered plesiomorphic even though the character is variable in the Melittidae.

106. Vein cu-v of hind wing: (0) Shorter than second abscissa of vein M, transverse or slanting. (1) About as long as second abscissa of vein M, slanting. (2) Over twice as long as second abscissa of vein M, slanting.

107. Gradulus of T2: (0) Directed backward above and behind spiracle. (1) Directed toward or reaching spiracle. (2) Absent.

108. Base of T2: (0) Without phragma-like apodeme. (1) With transverse, phragmalike apodeme. State (1) occurs in certain Xylocopinae and *Lithurge*.

109. Gradulus of S2: (0) Straight across medially or slightly curved posteriorly in middle. (1) Bisinuate, i.e., with two posteriorly convex curves. (2) Absent. Although most Melittidae have State (2), *Hesperapis* shows State (0) as do most other S-T bees.

110. Metasomal sternal scopa (female): (0) Absent. (1) Present. State (1) is principally a character of Megachilidae but certain oil-collecting bees (e.g., *Ctenoplectra*, *Tapinotaspis*) were also coded (1) although the sternal hairs function in gathering oil rather than pollen and probably evolved independently from those of megachilids.

111. Apex of S6 of female: (0) Entire or gently bilobed. (1) Emarginate, with lateral projecting lobes (Roig-Alsina, 1991, Figs. 11-13). State (1) is found only in Nomadinae.

112. Apex of S6 of female: (0) Without specialized coarse setae. (1) With groups of spinelike setae (Roig-Alsina, 1991, Figs. 3-10). State (1) is found in Nomadinae and Isepeolini.

113. Surface of T5 of female: (0) With prepygidial fimbria, hairs denser and longer than in hair bands of preceding terga. (1) Without prepygidial fimbria, i.e., similar to preceding terga.

114. Apex of T5 of female: (0) With polished margin of tergum absent or narrow and parallel-sided. (1) With broad, bare, polished margin wider in middle, margined basally by long, stiff setae.

115. T5 of female: (0) Without pseudopygidial area. (1) With pseudopygidial area. State (1) requires State (1) of Character 113.

116. Pygidial plate of T6 of female: (0) Present. (1) Absent.

117. T6 of female: (0) Not papillate. (1) Papillate or minutely roughened, dorsal surface hairless. State (1) is found only in the Fideliinae. In *Neofidelia* and *Parafidelia* the papillate area is the enlarged pygidial plate; this is probably also true for *Pararhophites*.

118. Pygidial plate of T7 of male: (0) Present, distinct. (1) Absent, but sclerotized apical rim suggests apex of plate. (2) Absent, without apical rim. This character varies among melittids but the presence of a pygidial plate is so widespread among other S-T bees that it is probably plesiomorphic. An alternative case, however, can be made for the repeated origin of this plate in males. Most females have a plate on T6; in both sexes it is on the last exposed tergum. The presence of the plate is clearly the plesiomorphic state in females (Character 116); it has a function in nest construction. Probably it is functionless in males. It might appear in males simply as a result of a regulatory change, which could occur independently in different lineages.

119. Apex of T7 of male: (0) Entire. (1) With two conical points.

120. S7 of male: (0) With two or four apical lobes. (1) Without apical lobes. (2) Short and transverse, without lobes. (3) Disc to whole sternum membranous.

121. S8 of male: (0) With single apical projection and moderate basolateral arms. (1) Without apical projection. (2) Bilobed apically. (3) Almost completely absent (in Meliponinae).

122. Gonobase: (0) Forming a complete ring. (1) Not evident ventrally (absent or possibly fused to gonocoxites). (2) Almost absent.

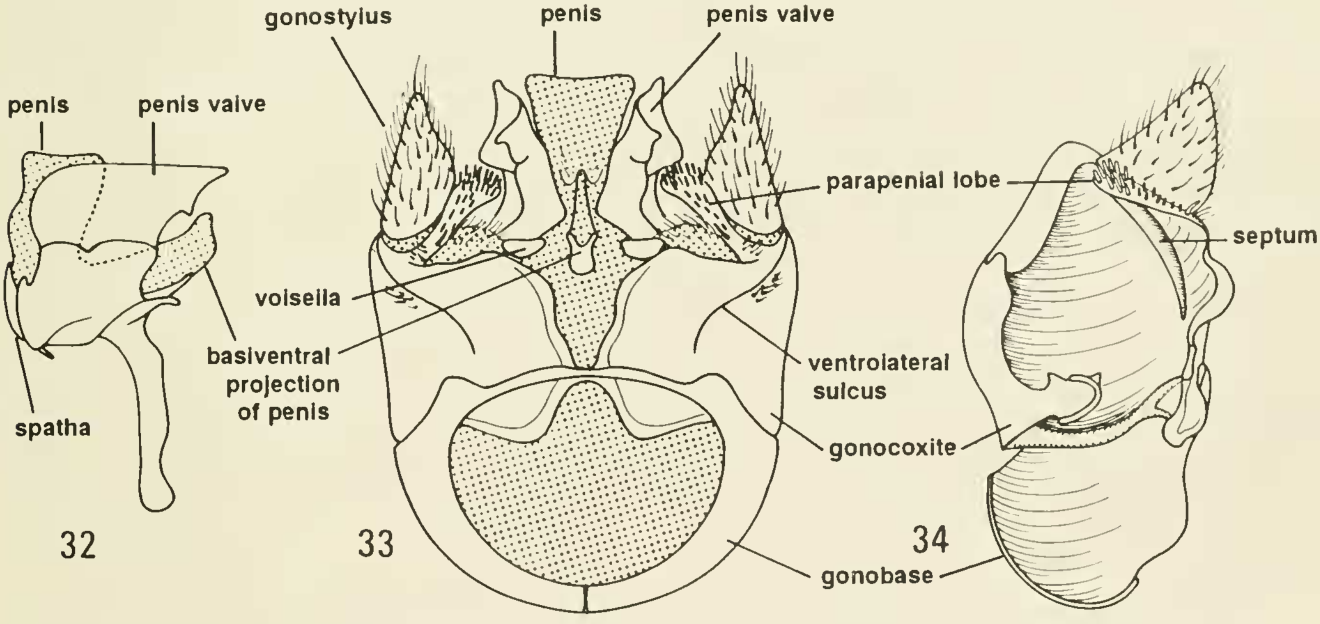
123. Gonocoxite: (0) Without sulcus or septum. (1) With ventrolateral oblique sulcus but no septum. (2) With septum, represented externally by sulcus, separating basal and apical parts of gonocoxite (Figs. 33, 34).

124. Ventral parapenial lobe of gonocoxite: (0) Absent. (1) Present, without strong setae. (2) Present, with strong, often peglike setae (Figs. 33, 34). This lobe is the ventroapical plate of Allodapini (Michener, 1975).

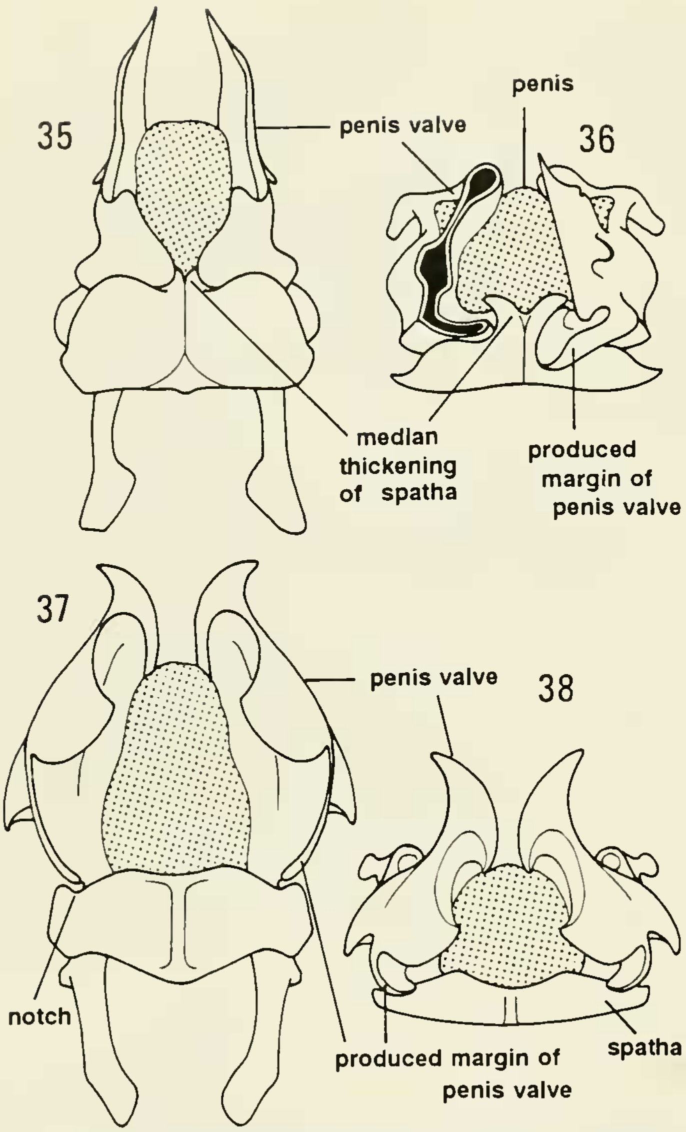
125. Gonostylus: (0) Articulated to gonocoxite although often with partial fusion (Fig. 33). (1) More or less indistinguishably fused to gonostylus (or absent?), the resulting structure being called gonoforceps. (2) Double, there being two nearly independent gonostylar structures arising from gonocoxite. This character is variable (0 or 1) among melittids and other S-T bees. The decision as to polarization is based largely on the morphological viewpoint that articulation must be primitive in insects.

126. Volsella: (0) Distinct, chelate. (1) A free sclerite but not chelate (Fig. 33). (2) Absent or fused to gonocoxite. The (0) state is as in most melittids as well as many other S-T bees.

127. Dorsal bridge of penis valves: (0) Short, not extended behind level of apodemes, or absent. (1) Expanded posteriorly as spatha (Figs. 35, 37).



Figs. 32-34. *Hexepeolus rhodogyne*, male genitalia. **32.** Penis and penis valve, lateral view. **33.** Genital capsule, ventral view. **34.** Internal view of right half of genital capsule, muscles removed to show septum.



Figs. 35-38. Penis valves and penis. **35.** *Tapinotaspis tucumana*, dorsal view. **36.** *Tapinotaspis tucumana*, apical view; one penis valve sectioned to show fit of its produced margin with median thickening of spatha. **37.** *Peponapis fervens*, dorsal view. **38.** *Peponapis fervens*, apical view.

128. Dorsal bridge of penis valves or spatha: (0) Lacking notches into which fit dorsal basal produced margins of penis valves. (1) Distal margin (of spatha) with two notches into which fit produced basal margins of penis valves (Figs. 37, 38). (2) Ventral surface of spatha with median thickening, lateral margin of which overhangs to form space into which fits produced basal margin of penis valve (Figs. 35, 36).

129. Penis with basiventral membranous projection: (0) Absent. (1) Present (Figs. 32, 33).

130. Base of gonostylus: (0) Not extending basad. (1) Extending basad on inner surface of gonocoxite. State (1) is found only in Tetrapediini.

131. Number of ovarian follicles or testicular tubules: (0) Three. (1) Four. (2) Five or more. Not many melittids have been examined for this character, but all S-T bees studied have State (0). State (2) is found only in some parasitic bees which have 5 to 13 and in *Apis*, which is very different, with 2 to 12 in workers, over 150 in queens.

Table 2 shows the states of the adult characters for the species listed in Table 1.

SELECTION AND CODING OF CHARACTERS OF MATURE LARVAE

The characters that we analyzed are those listed by McGinley (1981) that varied among L-T bees, and for which the plesiomorphic state was identifiable. Some were listed by McGinley (1981, Table 2) as "Cladistic Characters"; for others we believe the polarity is clear for L-T bees even though McGinley did not consider it clear for bees as a whole. For a few that McGinley considered "Cladistic Characters," we found polarity dubious for L-T bees; we excluded them from our list of characters. As with adult characters, plesiomorphic states were recognized usually using melittids as an outgroup. If there was variation among melittids, however, other S-T bees (colletids, andrenids) were used as a secondary outgroup. Moreover, if the other S-T bees differed as a whole from melittids, we concluded that the melittids probably had a family-level apomorphy, and considered that the other S-T bees exhibited the plesiomorphic condition for our study. Our judgment as to the plesiomorphic state sometimes differed from McGinley's because our outgroups are different; he dealt with bees as a whole while we are concerned with L-T bees. In some cases there are reasons to doubt our decisions as to polarity; these are indicated in the list of characters and in the following paragraphs.

As discussed by Michener (1953), various characters of bee larvae seem to have more primitive states in most L-T bees than in most S-T bees, even though the reverse is true for various adult characters. That is, in L-T bees the states of such characters are more like structures found in more ancestral Hymenoptera or other insects. Examples are Characters 1 (setae on the head capsule) and 20 (size of the antennal papilla). In both cases, the better developed state (longer setae, slender projecting papilla) is no doubt plesiomorphic for Hymenoptera as a whole. The reverse may be true for aculeate Hymenoptera, since they presumably evolved from parasitoids (Whitfield, 1992) in which larval structures are greatly reduced. Be this as it may, all Melittidae except *Meganomia* have reduced head setae and moderately developed to absent antennal papillae. Since *Meganomia* has many derived adult features (Michener, 1981), it is unlikely to exhibit the basic melittid larval structure and we therefore regard the remaining members of the Melittidae as good indicators of the plesiomorphic states for the analysis of the L-T bees. We therefore coded reduced head setae and reduced antennal papillae as (0); that is, among L-T bees, development of longer setae and antennal papillae is derived. Character 48 (labial palpal length) is similar except that the deviant melittid is *Macropis*, also a melittid with many derived adult features. In all these cases most S-T bees exhibit the character state that we have coded as (0). Of course a frequent state is not necessarily ple-

Table 2. Matrix of Character States for Adults
The characters and states are explained in the Annotated List of Adult Characters.

	12345678911111111112222222222333333333344444444445555555555666666666677777777778888888888999999999911111111111111111111111111111111
	01234567890123456789012345678901234567890123456789012345678901234567890123456789012345678900000000001111111111222222222233
	01234567890123456789012345678901
Ancestor	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Eremapis	0021110100000200000200200010110001100011100100110112001000000000001000000110001000000000101000000000101000000010000000200010102 1000?
Teratogn	002011010000020000020020001011000110001110010011011200101000000000100000011000120000000201000210000001000000000000000100010102 1100?
Isomalop	002011010000010010020020001011000110001110010011011200100000100001010000011001020000000201000210000101000000000000000101110102 1000?
Exomalop	002010010000000000010120001011000110001110010011011200100000100000101100011001010000000201000210000001000000000000000100210102 10001
Tapinota	002010010000020000021110001011010110001110010011011200101000110000101111020001021000000211000110000001102000010000000000210102 1200?
Tapinorh	000010010000020000021020001011010110001110010111011200101000110000101111021001021000000211000110000001010000000000000000210102 1200?
Arhysoce	001011010000020000021020001011010111001110010011011200101000110000201111121001011000000211000210000020100000000000000200210102 1200?
Paratetr	001111010000020000020020001011010111001110010011011201101000110000201111121001020000000110000210000020100000000000000200210102 12001
Monoeca	001010010000020000022020001011000111001110010011011200101000110000101011111001011000000011211210000020100000000000000001210102 1200?
Caenonom	001010010000020000022020001011010110001110010011011211100000010000211211021001021000000210100010100000202010000000000000210102 1200?
Ancylosc	001111010110020100022020001011000110001110010110011200101000100001100101121000010000000201000010000001000000000000000200210112 10001
Malitoma	0010110100100101000220210010110111110 01?111001001012001010001000011012011210010200000000201000000000001000000000000000002102101021200?
Diadasia	001011010010020100020020001011011110001110010110011200101000100001101201021001020000000201000000000001000000000000000002102101021200 1
Diadasin	001011010010020100020020001011011111001?111101011101120010000010000110110112100102000000001010000000000001000000000000000021021010212 00?
Ptilothr	000011010010020100020020001011011111001?111101011001120010100010000110120112100112000000010100000010000100000000000000000210210102120 01
Tetraped	000011010000010000020110001011000111001111001001011120010000010000010120102100100120000002110011010000102010000000000000211010012000 1?
Coelioxo	00001101001000010012011000100100?110001111101001011120010000010000030120102100100001000002110001010000010200?00001000021100002100 01?
Tarsalia	00?0100101000200000022020001011000111000111011001111120110000011000?1?10000?1?01010000000020100011000000221 00?00000000021001120210 00?
Eucerino	0010100101010?00000?20200010110001100001110010010111210101000 10?00?1?10000?1?01020000000211000110000001010 0?0000000000200210202100 0?
Canephor	0111100101010101000210200010110001011001110010010111200102000100000100001021001000001000211000011100101200000000000000000102021100?
Eucera	0011100101010100000220200010110001101001110010110111121010200011000011010102100102000000022100011000100121000100000000000001020211001
Melissod	001110010101010000022020001011000110000111001001011121010200011000010100102100102000000022100011000000022000010000000000000210202110 01
Svastra	0011100101010100000220200010110001101001110010110111121010200011000010110102100102000000002110001100000001200001000000000000010202100 01
Peponapi	001111010101010100022020001011000110101111001011011112101020001100001111010210010200000002210000100000001200001000000000000021020211 001
Anthopho	0010110100000000000220200011110001100000210110010111200100000001000200000113110100000000000210000020000112211000000000000021101000200 001
Habropod	0010110100000000010022020001111000100000021001001011110?01000000010002000001131101000000000002100000200001021110000000000000201010022 00001
Deltopti	111011010000000000002202100111000011000002100100101112111000000001000100000113111010000000000022000002000010211000000000000002110101210 000?
Centris	000010010000000000020010001011000110000011011001011121010000010100010010111310011010000000110111010100112200000000000000002110101220 0001
Epichari	0000110100000010000021020001011000111000011011001011221010000010100011000102100102100000001102111201000022100000000000000000001012121 1000?
Xeromele	000011010000001000002202000100100000000011210010010111100101000001000011210011200100001010000100001121120000000110002111121011000?
Zacosmia	000011010000000000002212000100000?110001121001001011111010100030000112100012001000010100000010011211200000001100000001120010000 1
Thyreus	000011110000000000002212000100100?10000112100120101111101010010002000012210011200100000010000101001121120000000110002102121011 0001
Ericroci	000011010100000000001200200010010 0?1010001211010010111121011000100100001121000100010000000020000000011112220200010000211112102 00002
Mesonych	0000110101000100001201200010010001000001211010010111210110000000100100101221000100010000000200010000112122202000100002111121010000?
Mesoplia	0000110101000000000120120001001000111001121101001011121011000001001001012210001000100000002000100001121122202000100002111121020000 1
Rhathymu	00001101010001000012002000100100?11000111111101011111010000000100100001121001100010000001000210000002021000000100002110111221000?
Parepeol	00001101000001000002111010101100011000011100100100112001000000000200101021000100010000001000001000002020000000011000001012121 1000?
Ecclitod	00001101000000010002102010100100011000011100100100112001000000000300101021000100010000001000001000000202000000001100000101212110 00?
Osiris	00011101000000000001201201010110001100011100100100112001000000000200001031000100010000000100000100000000200000000110002011100011000?
Leiopodu	00001101000000000012002000100100011001?111100101100112001000010002000010210011000100001010000000000000101000000001010020111001200 00?
Isepeolu	000011010000000000122020001001000110000111001001011120010000010000000011210001000100000210000000000111010000000010010101100001100 0?
Melectoi	000011010000000000122020001000000110001110010010111200100000010001000010210001000100001210000000000101010000000110010101010001100 0?
Neolarra	0000110100000000001020100001000000011001011100100110111001000000000200000021000100010000001000000000111?02000001010000000101220110102
Caenopro	0000011100000000100020100001000000011000111110100100111001000000000000113100010001000000000000000001001020100010100002111100120000 2
Oreopasi	0101111100000001100020100001000000110000111001201001110010000000000200102100110001000000010000000010010201000101001000110000200002
Triepeol	0001110100000000000021100001000000100001121001001011010010000000200001121001100010000000100000000000202000001110100001010001001 02
Epeolus	0001110100000000000021000001000000100001121001001011010010000000100001131000100010000000100000000001202000001110100001011002001 02
Rhogepeo	00011101000000000000211000010000001000011210010010110200100000000200001121001100010000000100000000000020200000111010000101210110 00?
Holcopas	000011110000000000102010000100000001100011110010010010100100000002000011310001000100000001000000000100202000001110100001010012000 02
Brachyno	00001101000000110102010000100000001100011110010010010100100000000200001121001100010000000100000000000000200000111010000101212110 00?
Kelita	000011010000000101020100001000000011000111100100101 1?200100000000201000021001100010000000100000000000000200000111010000101222110102
Pachynom	000110010000000110102010000100000001100001110010011010100100000002000011010001000100000001000000000000002000000110100000101220110 00?
Centriae	000111010000001101120100001000000011000011100100110100001000000002000011010001000100000001000000000000002010000110100001011002100 02
Biastes	00001101000000011102010000100000011000011100100100100001000010003000010210001000100000001000000000100202000001110110001002202101 0?
Hexepeol	00001101000000000010201000010000001100001211010010010100100000001000010210001000000000001000000000000020200000111010000110220110102
Manuelia	0000100001000011000101000010100001100011110010011011200100001000100001011000100000000010100000000000001020100000100002020101021000 1
Xylocopa	0000100001000100000000101001010010100001101101001001121110000000001000010210011000000000101000020100101210000000100002021100121000 1
Ceratina	0100100101000011000201010010110001100011110010010011200100101000100000021000120000000000100000000000002010110000100102021100121000 1
Macrogal	0100100101000011000?00010010000000101001111001001001120010010100011000002100010000000000010000000001002000110000100102021101021000?
Brauneap	010011010100001100020101001000000111001111001011001120010010010001100000210001000100000001000000000100000011000010010202110202100 01
Bombus	00000101000001001002002000101000011000101110110101112001000100100001001112010111200111110110002101000021300000001001020101000110001
Apis	0000001000001011002012000001000011001?011101201001220010001101021010000120101111??2111110110002100000023002000001001020212001200002
Melipona	0000000100000101100201200010000001100000111012010112200100011011210100111201001 1??2111101110000100020033001000001001020132000210001
Partamon	0100000100000?011002012000100100?1100000111012010012200100011011210100011120100 11??211110111000010012003010100001001020132000210001
Euglossa	0101110100001?00000220210010110001110000110110010111121110001001000011010122101112101111111100021010000222000000100102010100011 0001
Eufriese	0101110101001?0010022011001011 00?1110000110110010111121110001001000011010122101112101111101110021010000223000000100102010100011000?
Pararhop	0000000010000001000000200010000001110000110010011011201100000100000300000021001100110000001100000011010000000100110111010000100 0000
Neofidel	00101011100000000000001000101000010000102100100100112001000001000000001021000100110000001100000000101100000010011001001000000000 0?
Parafide	001000001000000010002 0?10001000000010110?02100110101112001000011?00???10011?1?011001100000112000000010110 00?0100110010000000100000?
Lithurge	10000010100000010000000100001000100111001011101000101120110001000003010010210011000000010000000111001000010100100000001100012000 0?
Trachusa	1001001100000011000001000010001001110010110010010011200100011000031000112100110001000000110001000010022001001001001020110000200 00?
Anthidiu	100000110000001100000100001010100111000011001001001120010001100003000011110011000100000001000100101002210100100100102010000002 00000
Hoplitis	10010010100000110000000000010001001110010110010010011200100001000003000000110001000100000001000000011002120100100100102010100010 000?
Osmia	1001001010000010000001000010001001110010111010010011200100011010030000111100010001000000210000000110021101001001001020300001100000 0
Megachil	10010011100000100000010000100010011100101100100100112001000100000003000011210001000100000110000001110021101001001001020300001200000 0
Coelioxy	1001001100000010000211000010001 0?1110010110010010011200100010000000003000011210001000100000010000001110021100000000100102030000120000 0
Ctenople	0100110100000200000120100010110001000001010000000000200101000101000100?0210010010000101110001001010020000000100000002002100021000?
Macropis	00001000000000000000001100000000000000010000000000000 0??00000001010003000000000000000000001000000100010000000002000000000000000000000 0
Melitta	0000100000000000000020100110010000000000000010000000000000??00000001000300001000000000000000020000000000000000000000200000000000000010000 0?
Dasypoda	00001000010000000002000011000000000000000010000000000000110000001000310001000000000000010000000100000000100001000200000000200000000000 00?
Hesperap	00001000000000000000200000100000000000000000100000000000000000??0000100031000000000000000000000010000000100000000000000000000000010000 00
Meganomi	00001000000000000000202001100000000000000000100000000000000000??00001000310001020000000000000000000010000000210000200000000000000000011000 00

siomorphic, but we believe that in these cases the plesiomorphic condition for L-T bees is widespread in S-T bees; any alternative negates the use of Melittidae as the closest outgroup and sister group of L-T bees.

For several other characters (43, 44, 46, 47, 49) the situation is less clear because there is less unanimity in the Melittidae, and melittids with more plesiomorphic character states such as *Melitta* sometimes have the more fully developed structures. However, since these characters are probably all functionally related in bees (in connection with cocoon spinning, see below), we believe that they have to be treated like Characters 1, 20, and 48, i.e., with the reduced condition being considered ancestral for L-T bees.

To summarize, other authors considered the better developed states of the characters listed above as ancestral and the reduced states as apomorphic. They were considering bees as a whole. For L-T bees only, we must reverse the polarity, in view of evidence from Melittidae, our first outgroup. In addition, if aculeates arose from parasitoids that show the reduced states, we believe that the polarity that we advocate for L-T bees may be appropriate for all bees. Reversions from the reduced states to more developed states may have occurred independently in various aculeate groups such as bees, sphecoid wasps, etc.

Most or all of the characters listed above may relate to cocoon spinning or the sensory apparatus needed for cocoon spinning. In L-T bees, taxa that do not spin cocoons, like the Nomadinae, Xylocopinae, and Anthophorini, have (secondarily) reduced states for these characters, although most L-T bees have the better developed states and spin cocoons. Most S-T bees do not spin cocoons and have the reduced states. However, it is obvious that developed states of these characters are not always associated with cocoon spinning. For example, many parasitoids spin cocoons although they have extremely reduced cephalic structures. Moreover, the cocoon-spinning S-T bees (Diphaglossinae in the Colletidae, Rophitinae in the Halictidae and some Melittidae) are equivocal in development of these structures; for example in the Diphaglossinae, antennal papillae are small, galeae are absent, but palpi are rather long.

One could argue that, if the above explanation is correct, one should list only a single character, rather than overweighting it with several manifestations thereof. However, none of the characters are perfectly correlated; each provides some different information. Given our present knowledge of insect development, it seems unwise to do more than note this situation. We suspect that many other characters are also not independent.

That cocoon spinning, involving silk production and spinning behavior, would evolve, after having once been lost, seems less likely than redevelopment of the individual structural features discussed above. There are therefore legitimate differences of opinion as to polarities. The subject deserves restudy by persons thoroughly familiar with bee larval characters.

ANNOTATED LIST OF LARVAL CHARACTERS

These characters are more fully explained by McGinley (1981). The number of each character is followed by McGinley's number in parentheses.

1 (1). Setae on head capsule: (0) Short and difficult to see. (1) Long and distinct. All melittids except *Meganomia*, which is probably a derived melittid, and many other S-T bees, have State (0), which we tentatively consider plesiomorphic for L-T bees, although presence of long setae must be plesiomorphic for aculeate Hymenoptera.

2 (2). Spiculation on dorsal surface of labrum: (0) Absent. (1) Present. Most melittids, all colletids and halictids, and some andrenids have State (0), which we tentatively consider plesiomorphic.

3 (3). Epipharyngeal spiculation: (0) Present. (1) Absent.

4 (4). Hypopharyngeal spiculation: (0) Present. (1) Absent.

5 (5). Dorsal and mesal maxillary spiculation: (0) Present. (1) Absent.

6 (6). Pigmentation of head: (0) Light. (1) Heavy. State (1) is known, among L-T bees, only in certain Nomadinae.

7 (9). Vertex: (0) Rounded. (1) Produced forward.

8 (10). Swelling above antennae: (0) Absent. (1) Present.

9 (14). Anterior tentorial pit: (0) High. (1) Low. McGinley's (1981) States 2 and 3 are lumped and coded (0); his State 1 is coded (1). All mellitids have State (0), as do most colletids and the genus *Andrena*. We therefore think that our polarity is appropriate for a study of L-T bees.

10 (15). Posterior tentorial pit: (0) At junction of hypostomal ridge and posterior thickening of head wall. (1) Anterior to or below this point. Among L-T bees, State (1) is found only in Nomadinae.

11 (16). Posterior thickening of head wall: (0) Well developed. (1) Weakly developed. (2) Absent medially.

12 (17). Median portion of posterior thickening of head wall: (0) Straight. (1) Curving forward.

13 (18). Posterior thickening of head wall: (0) Single. (1) Appearing double.

14 (19). Median longitudinal thickening of head wall: (0) Absent. (1) Developed only dorsally. (2) Extending forward to level of epistomal suture. Since nearly all colletids and andrenids have State (0), as do all melittids except *Meganomia*, which has State (1), and State (2) is found only in some L-T bees, we consider State (0) plesiomorphic. It is possible, however, that State (1) is plesiomorphic instead of State (0).

15 (20). Hypostomal ridge: (0) Well developed. (1) Weak.

16 (21). Hypostomal ridge: (0) Simple. (1) Divided posteriorly. State (1) is known only in certain megachilids.

17 (23). Angle of hypostomal ridge to posterior thickening of head wall: (0) Obtuse. (1) Perpendicular.

18 (24). Pleurostomal ridge: (0) Well developed. (1) Weak.

19 (26). Epistomal ridge or depression: (0) Well below level of antennae. (1) Arched upward to or above antennal level.

20 (30). Antennal papilla: (0) Enlarged basally and moderately developed to virtually absent. (1) Well developed, slender and projecting. Although it makes sense to believe that reduction of larval antennae might be a progressive process, all S-T bees except *Meganomia*, a derived melittid, have State (0), while many L-T bees have the better developed antenna of State (1).

21 (31). Number of antennal papillar sensilla: (0) 2-5. (1) More than 5. State (1) is found only in certain parasitic Anthophorinae.

22 (32). Clypeal length: (0) Moderate to long. (1) Short.

23 (33). Frontoclypeal area, in lateral view: (0) Not strongly produced. (1) Rounded, greatly produced. Among all bees, State (1) is found only in two nomadine genera and two melittid genera. [As elsewhere, this statement is based on McGinley's (1981) matrix; a third nomadine genus is now known to show State (1) (Rozen and McGinley, 1991).]

24 (34). Labrum in lateral view: (0) Moderately projecting beyond clypeus. (1) Strongly projecting. Among L-T bees State (1) is found only in Nomadinae.

25 (35). Labral tubercles: (0) Present, well defined. (1) Absent or poorly defined. This relates to the two rounded marginal tubercles. The pointed tubercles on the disc of the labrum found in Nomadinae are evidently not homologous (J. Rozen, in litt., 1993). Although melittids have State (1), State (0) is characteristic of nearly all andrenids, halictids and colletids and is therefore considered plesiomorphic; presumably State (1) is an apomorphy of melittids.

26 (39). Sensilla-bearing swellings on labral apex: (0) Present. (1) Absent. Because such swellings are present in most bees including our outgroups, we have reversed the polarity indicated by McGinley.

27 (40). Epipharynx: (0) Not produced. (1) Produced as distinct lobe. State (1) is found only in two genera of Nomadinae.

28 (44, 45). Mandibular spicules: (0) Absent or short. (1) Long and hairlike.

29 (47). Mandibular apex, ignoring teeth if present: (0) Acute. (1) Broadly rounded or truncate.

30 (48, 49). Mandibular apex: (0) Simple. (1) Bidentate with

dorsal tooth longer or teeth subequal. (2) Bidentate with ventral tooth longer. All colletids and most andrenids, halictids, and melittids have State (0), which we therefore consider ancestral. The polarity is tentative; given the multiple teeth of wasps, one would expect two teeth to be ancestral to one.

31 (51). Apical part of mandible: (0) Not attenuate. (1) Attenuate.

32 (52). Mandibular cusp: (0) Well or moderately defined and produced. (1) Weakly defined or absent.

33 (53). Cuspal projection of mandible: (0) Absent. (1) Present.

34 (54). Mandibular cusp: (0) Multidentate. (1) Smooth, edentate.

35 (55). Teeth on dorsal apical edge of mandible: (0) Present. (1) Absent.

36 (56). Ridge delimiting apical mandibular concavity: (0) Hidden from above by dorsal apical edge. (1) Visible from above, exceeding dorsal apical edge.

37 (57). Mandibular apical concavity: (0) Weakly to moderately developed. (1) Strongly developed.

38 (58). Mandibular concavity: (0) Oblique, not scooplike. (1) Scooplike.

39 (61). Labiomaxillary region: (0) Moderately recessed. (1) Produced. (2) Strongly recessed. All andrenids and many members of all other S-T families including half of the melittids have State (0), which is tentatively considered plesiomorphic for L-T bees. Our treatment here is similar to that of other characters that seem to be associated with cocoon spinning. (See sections on Selection and Coding of Characters of Mature Larvae.) McGinley (1981) and J. Rozen (in litt., 1993) regard State (1), produced, as ancestral but for the reasons indicated we suspect that the intermediate condition, State (0), is ancestral for this study.

40 (62). Labium and maxilla: (0) Distinct. (1) Fused.

41 (63). Labium: (0) Exceeded in length by maxilla. (1) Subequal to maxilla. (2) Exceeding maxilla.

42 (65). Inner apical maxillary surface: (0) Rounded. (1) Produced mesally. In all Andrenidae, nearly all colletids, and melittids except *Dasypoda*, State (0) is found. We therefore have changed McGinley's polarization for the study of L-T bees.

43 (68, 69). Maxillary palpus: (0) Elongate, usually twice as long as basal diameter. (1) Apparently absent. (2) Shorter than basal diameter.

44 (70). Maxillary palpus: (0) Slender. (1) Robust. Since State (0) is found in all andrenids and many colletids, and in half the melittid genera listed by McGinley, it is tentatively regarded as plesiomorphic.

45 (71). Location of maxillary palpus on maxilla: (0) Apical. (1) Dorsal. (2) Ventral. State (0) characterizes all but one melittid and considerable numbers of colletids and andrenids. It is therefore tentatively regarded as plesiomorphic.

46 (72). Galea: (0) Absent. (1) Present. Nearly all S-T bees except three melittid genera lack the galea, while it is present in many L-T bees. See discussion in the section on selection and coding of larval characters.

47 (73). Labial division into prementum and postmentum: (0) Weak or absent. (1) Strong. All andrenids, nearly all halictids, and about half the colletids have State (0), which also occurs in the melittids *Hesperapis* and *Capicola*. We tentatively accept the polarity indicated. This character is largely associated with Character 39 and the same comments apply to both.

48 (76). Labial palpus: (0) Shorter than maxillary palpus. (1) Subequal to or longer than maxillary palpus. State (0) occurs in all andrenids, most colletids, and all but *Macropis* in the Melittidae. This state is therefore considered plesiomorphic for L-T bees.

49 (77). Salivary lips: (0) Greatly reduced or absent. (1) Well developed. Although variable in melittids, the presence of State (0) in all andrenids and nearly all colletids and halictids suggests the polarity indicated.

50 (79). Salivary opening: (0) Transverse. (1) Recurved. (2) Circular or oval. All the melittids have State (0). Other S-T bees mostly have states not represented among L-T bees, although some colletids have State (0).

51 (80). Salivary opening: (0) Nearly as broad as distance between labial palpi or broader. (1) Much narrower. Although melittids are variable, all andrenids and halictids and all colletids except *Colletes* have State (0), which is therefore considered plesiomorphic.

52 (81). Position of salivary opening on labium: (0) Apical. (1) Dorsal. State (1) is found only in Xylocopinae.

53 (84). Hypopharyngeal size: (0) Normal. (1) Enlarged. Among L-T bees, State (1) occurs only in certain parasitic bees.

54 (85). Apex of hypopharynx: (0) Rounded. (1) Bilobed. Although variable in melittids, this character is as State (0) in all halictids and andrenids and nearly all colletids.

55 (87). Hypophyrangeal groove: (0) Distinct. (1) Absent or indistinct.

56 (88). Body integument: (0) With patches or transverse rows of conspicuous spicules or setae. (1) Without conspicuous spicules or setae. Rozen (1987, p. 8) showed that this and the next character, as treated by McGinley (1981), require restatement. While constrained by the character states as recorded by McGinley, we have tried to word the characters in ways that remain meaningful for analysis. The "setae" of many megachilids are primarily elongate, erect spicules. A few true setae are intermixed, and are as long as the spicules. The hairy appearance of most megachilid larvae is a strong apomorphy (Character 57). Character 56 has to do with patches or rows of spicules and setae, mostly directed backward, not comparable to the generally distributed erect hairs found on many megachilids.

57 (89). Body integument: (0) Apparently nonsetose. (1) Seemingly conspicuously setose. Sphecids and most megachilids are conspicuously hairy, and as pointed out by McGinley (1981) and Michener (1953), this should be the plesiomorphic state. However, near absence of hairs in all S-T bees except certain melittids requires us to polarize this character as indicated above, implying a reversion in megachilids. Presence of hairs in most allodapine larvae shows that they can appear in lines that nearly lack them.

58 (92). Paired dorsal darkened areas on thoracic segments: (0) Absent. (1) Faintly evident.

59 (93). Body length: (0) Moderate. (1) Long.

60 (94). Body form: (0) Robust to moderately robust. (1) Slender.

61 (95). Body, as seen in side view: (0) Widest medially. (1) Widest posteriorly.

62 (101). Median dorsal abdominal tubercles: (0) Absent. (1) Present.

63 (102). Dorsal conical tubercles, two per segment, usually darkened and pointed, on thorax and at least first abdominal segment: (0) Absent. (1) Present.

64 (105). Venter of abdominal segment IX: (0) Not protuberant. (1) Protuberant.

65 (106). Length of abdominal segment X: (0) Moderate. (1) Long. (2) Short.

66 (109). Venter of abdominal segment X: (0) Rounded, not produced. (1) Produced. This character is sufficiently variable among S-T bees that the polarity has to be considered doubtful.

67 (111). Dorsum of abdominal segment X: (0) Without transverse line or ridge. (1) With transverse ridge. (2) With transverse line. This character varies in Melittidae but shows State (0) in all Andrenidae and nearly all Colletidae.

68 (113). Anus positioned: (0) Apically. (1) Dorsally. (2) Ventrally.

69 (116). Spiracular sclerites: (0) Absent. (1) Present.

70 (117). Spiracular atrial shape: (0) Subglobular to subquadrate to broad and rounded. (1) Very broad and shallow. Because State (0) occurs in all mellitids and andrenids as well as some colletids, we consider it plesiomorphic for L-T bees.

71 (118). Spiracular atrium: (0) Not or little produced above body surface. (1) Strongly produced. State (0) is found in almost all S-T bees except some melittids.

72 (119). Spiracular atrial wall: (0) Not ridged. (1) Ridged.

73 (120). Spiracular atrial wall: (0) Without spines. (1) With small spines or denticles. (2) With long spines. Spines or denticles are widespread and may be plesiomorphic for bees as a whole, but since all andrenids, nearly all melittids, and many colletids have State (0), we consider it plesiomorphic for this study.

74 (121). Spiracular atrial rim: (0) Present. (1) Absent.

75 (122). Width of spiracular peritreme: (0) Narrow (even absent) to moderate. (1) Very wide.

76 (125). Primary tracheal collar: (0) Smooth. (1) Spinose.

77 (126). Spiracular subatrial length: (0) Moderate, more than two to four times atrial length. (1) Over four times atrial length. (2) Twice atrial length or less. Although all melittids except *Meganomia* have State (0), variability in other S-T bees makes our polarity for this character inconclusive.

Table 3 shows the states of the larval characters for the species included in this study.

PHYLOGENETIC ANALYSES

Computer analyses of exemplar species using data in the character matrices (Tables 2 and 3) were made with Hennig86 1.5 (Farris, 1988) running on a Zenith 386. Certain analyses were also made with PAUP 3.0g (Swofford, 1990) using heuristic search with TBR branch swapping and the Deltran option. The results were identical to those obtained with Hennig86. Analyses that resulted in more than one tree were each summarized by a consensus tree using Hennig86.

Maddison (1991) has demonstrated that sometimes multiple islands of minimum-length trees exist and that not all of them are found in simple analyses. Therefore, using the trees produced by the algorithms h, h*, m, and m* provided by the Hennig86 program and two arbitrarily constructed trees, a multiple search for minimum-length trees was made applying the branch swapping algorithm bb*. For most analyses a single set of such trees was obtained, but in the study of larvae (Analysis E) two islands of trees were found.

In studying the cladograms, and seeing that a character state appears at two or more widely different places, it is tempting to re-examine the characters, discern differences between apparently distantly related possessors of a given state, and decide to make two or more characters, thus eliminating apparent convergence. We have done very little of this, although the result would have been cladograms with higher consistency indices. This sort of activity is likely to be highly subjective, because with the desire to improve the tree, one can often find differences between similar structures in different clades that can be interpreted as indications of independent origins. It seems better not to engage in such potentially circular activity except in the clearest cases. See also Concluding Remarks.

In the analyses presented below, we have not introduced differential weighting of characters. To do so *ad hoc* is arbitrary. We tried the successive weighting option of Hennig86 but as might be anticipated, it accentuated the predominance of correlated characters related to the parasitic way of life.

Within most of the analyses (A to H) the various minimum-length trees were similar to one another in the topology of larger units and to a considerable extent were fully resolved. We therefore selected a minimum-length tree for presentation of some of the analyses. When such trees differ, resulting in polytomies in consensus trees, the matter is mentioned below, as are the two islands of trees in Analysis E.

The following is a list of the analyses:

Analysis A was based on the full matrix (82 taxa, 131 characters) of adult characters. (See Table 1 for list of taxa, List of Adult Characters for character state codes, and Table 2 for the matrix.) Tree length (L) was 894, number of minimum-length trees (T) was 756, consistency index (ci) was 19, retention index (ri) was 65. One of these trees is shown as Cladograms 1a and 1b. After the first branch swapping a full buffer prevented further swapping. For this reason Analysis B was performed.

Analysis B was based on a matrix reduced in information content by collapsing to polytomies four groups, namely, Melittidae (Cladograms 1a, 1b, Node 2), Megachilinae (Node 7), Emphorina (node above 34), and Eucerini (node above 39). Collapsing was done by changing characters of taxa that varied within the group to the state found in the root of the group in Analysis A. When the state of a character in the root was equivocal it was not changed. Thus the matrix was the same size as for Analysis A but indicated much less diversity for the four groups listed. For Melittidae, character 73 was equivocal and character 100 was also not collapsed because to do so would have made two submarginal cells plesiomorphic, whereas we believe that three is the plesiomorphic condition. Other characters that were equivocal were, for Megachilinae, 79; for Emphorina, 21; and for Eucerini, 121. Statistics for Analysis B: L 762, T 270, ci 22, ri 70. There was no problem of a full buffer limiting swapping. No cladogram is provided to represent results of Analysis B because tree topologies were so similar to those of Analysis A.

Analysis C used the same modified matrix as for Analysis B, except that five characters (19, 29, 84, 105, and 113) that seem related to cleptoparasitism were omitted. The derived state of each of these characters is found only or largely among parasitic bees and the ancestral state among nonparasitic bees. This manipulation was made because in Analyses A and B, features characteristic of parasitic taxa appeared as ancestral for both parasitic and nonparasitic bees. We reject hypotheses that a nonparasitic bee could evolve from a parasitic ancestor, because of the parasites' loss of behavior and structures (like the pollen-carrying scopa) necessary for successful nest construction and provisioning. Statistics: L 719, T 176, ci 23, ri 70. The basal parts (i.e., to the tribal level but largely without genera) of one of the trees is shown as Cladogram 2a, and a simplified version in Cladogram 2b.

Analysis D used the matrix of Analysis A except that all cleptoparasitic taxa were omitted, resulting in 54 included taxa. Like Analysis C, this was an effort to determine whether the parasitic taxa were greatly influencing, because of convergence misinterpreted as homology, relationships shown among nonparasitic taxa. Statistics: L 628, T 1712 plus over-

Table 3. Matrix of Character States for Mature Larvae
The characters and states are explained in the Annotated List of Larval Characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macropis	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Melitta	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Dasypoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	2	1	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Capicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Meganomi	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Ctenople	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0	1	1	1	0	2	1	0	0	2	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	2
Stelis	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	2	0	1	0	1	0	0	1	1	1	0	1	1	0	0	2	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	2	0	0	1	0	1	0	1	2	0	0	0	2
Lithurge	1	0	1	1	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	2	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	2	0	0	?	2
Dioxys	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	2	1	1	0	1	0	0	0	0	1	0	2	1	0	0	2	0	1	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	2	0	0	?	0
Hoplitis	1	0	1	1	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	2	0	1	0	1	1	0	1	1	0	0	0	1	0	0	2	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1
Coelioxy	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	2	0	1	0	1	1	0	1	0	1	0	2	1	0	0	2	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	2	0	0	1	0	0	0	1	1	0	0	0	2
Trachusa	1	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	2	0	0	1	0	0	0	0	2	0	0	0	2
Megachil	1	0	1	1	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	2	0	0	0	1	1	0	1	1	1	0	1	1	0	0	2	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	2	0	0	1	0	0	0	1	2	0	0	?	2
Osmia	1	0	1	1	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	2	0	1	0	1	1	0	0	1	1	0	1	1	0	0	2	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	2	0	0	1	0	0	0	1	2	0	0	?	2
Anthidiu	1	0	1	1	1	0	0	0	1	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	0	1	1	0	2	1	0	0	2	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	2	0	0	1	0	0	0	1	0	0	0	?	0
Dianthid	1	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1	1	1	0	1	1	0	0	2	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	2	0	0	1	0	0	0	1	0	0	0	0	0
Ashmeadi	1	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	2	0	1	0	1	1	0	0	1	1	0	1	1	0	1	2	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	1	?	0	0	?	?	?	2
Fidelia	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	?	1	0	1	0	0	1	0	0	0	1	2	0	0	1	1	1	0	1	1	1	0	2	1	0	0	2	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	2	0	1	1	0	1	0	0	1	0	0	1	2
Neofidel	1	0	1	1	1	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	2	0	0	1	1	1	0	1	1	1	0	2	1	0	0	2	0	1	1	1	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	2	0	1	1	0	0	0	0	1	0	0	0	2
Parafide	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	1	0	0	0	1	2	0	0	1	1	1	0	1	1	1	0	2	1	0	0	2	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	2	0	1	1	0	1	0	0	1	0	0	1	2
Pararhop	0	0	1	1	1	0	0	0	1	0	0	1	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	2	1	1	1	1	1	0	0	1	1	0	2	1	0	0	2	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	1	0	1
Melecta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0	2	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	0	0	2
Thyreus	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	?	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	1	1	0	0	2	?	0	0	2	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	0	0	2
Zacosmia	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	2	?	2	0	0	0	0	0	1	1	1	0	0	0	?	1	?	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2
Rhathymu	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0	2	0	0	1	2	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	0	0	2	0	0	0	2
Acanthop	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0	2	0	0	1	0	0	1	0	1	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	2
Isepeolu	0	0	1	0	1	0	0	0	1	0	2	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	2	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Protepeo	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	1	0	1	0	0	1	1	1	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	?	1	?	?	?	?	?	?
Triepeol	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	2	0	2	1	2	0	0	0	0	2	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	2
Epeolus	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	2	1	2	0	2	1	2	0	0	0	0	2	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	2
Nomada	0	0	0	0	1	1	0	0	0	1	2	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0	0	1	0	0	0	0	0	2	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Oreopasi	0	0	1	1	1	0	0	0	0	1	2	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1	2	0	0	1	0	0	0	0	0	2	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0
Pseudodi	0	0	1	1	1	1	0	0	0	1	2	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1	1	0	2	1	0	0	0	0	0	2	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	2
Ammobate	0	0	1	1	1	1	0	0	0	1	2	0	1	1	1	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	2	1	2	0	2	1	2	0	0	0	0	2	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Morgania	0	0	1	1	1	1	0	0	0	1	2	0	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1	2	0	2	1	0	0	0	0	0	2	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0
Holcopas	0	0	0	0	1	0	0	0	0	1	2	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1	2	0	2	1	2	0	0	0	0	2	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Neopasit	0	0	1	1	0	0	0	0	0	1	2	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	2	1	2	0	1	?	?	0	0	?	0	2	1	0	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0
Neolarra	0	0	1	1	0	0	0	0	0	1	2	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	2	1	2	0	1	?	?	0	0	?	0	2	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	0	0	0	0
Xenoglos	1	1	0	1	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	0	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	1	1	0	0
Peponapi	1	1	0	1	0	0	0	0	1	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	1	1	0	0
Melanoma	0	0	0	0	0	0	1	1	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	2	1	2	0	0	0	2	0	0	0	0	2	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	2	0	0	0	2
Paranoma	0	0	0	0	0	0	1	1	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	2	1	2	0	0	0	2	0	0	0	0	2	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	2	0	0	0	0
Centris	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	1	1	1	0	2	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	2	0	0	1	0	0	0	1	0	1	0	0	0
Epichari	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	1	1	0	0	0	0	2	1	0	1	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	1	1	0	0	1	0
Habropod	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	0	0	0	1	2	1	0	0	0	0	0	1	1	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	2	0	0	1	0
Anthopho	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	2	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2	0	0	1	0
Diadasia	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0	2	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	2	0	1	1	0	0	0	0	0	0	0	0	2
Melitoma	1	0	1	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0	1	0	0	2	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2
Exomalop	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	2	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Xylocopa	1	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	1	1	1	0	1	1	2	0	0	0	1	0	0	2	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	0	0	1	0	0	0	1
Ceratina	1	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	1	0	2	0	0	1	0	0	0	2	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	0	?
Allodape	1	0	1	1	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	0	0	0	2	0	2	0	1	?	?	0	0	?	0	2	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	1	0	?	?	1	?	?	0	1
Paratetr	0	0	0	0	?	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	1	1	1	0	1	1	2	?	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0
Apis	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	2	0	2	0	2	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1
Bombus	1	0	1	0	1	0	0	0	1	0	0	1	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	2	0	1	0	1	1	0	1	1	1	0	2	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	2	1	0	1	0	1	1	1	0	0	1
Eufiesea	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	2	0	1	0	1	1	0	1	1	1	0	2	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	1	2	1	0	1	0	1	0	0	2	0	1
Melipona	1	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	0	1	1	0	2	0	2	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	1	0	0	1
Trigona	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0	?	1	0	2	0	2	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	1	0	0	1

flow, ci 26, ri 66. The consensus tree based on the 1712 trees is shown as Cladogram 3a.

F. A. Silveira repeated our Analysis D and then re-examined the relationships using successive approximations character weighting (Farris, 1969). Statistics: L 635, T 8, ci 26, ri 66. The topology different from that of the first part of Analysis D is presented in Cladogram 3b.

Analysis E was based on the matrix of characters of mature larvae (61 taxa, 77 characters). See Table 3 for the matrix and taxa and the List of Larval Characters for characters and states. Two islands of trees were found. For the larger island, the statistics are: L 482, T 176, ci 18, ri 67. The consensus tree is shown as Cladogram 4. The smaller island resulted in 16 trees, and otherwise the same statistics. As noted below, the trees of the smaller island were not useful and no cladogram representing them is presented.

In order to compare analyses based upon larval and adult features, we reduced matrices to include only taxa for which both character sets were available, as follows:

Analysis F was based on larval characters (47 taxa, 77 characters). Statistics: L 411, T 12, ci 21, ri 63.

Analysis G was based on adult characters (47 taxa, 131 characters). Statistics: L 625, T 940, ci 27, ri 62.

Analysis H was based on a matrix (47 taxa, 208 characters) consisting of both larval and adult characters, i.e., matrices for Analyses F and G combined. The taxa are those in common at the genus level between Analyses A and E, except that larval *Allodape* and adult *Braunsapis* characters constitute one taxon for purposes of Analysis H. Likewise adult *Biastes* and larval *Neopasites* were associated, as were adult *Nomada (Pachynomada)* and larval *Nomada* (*Nomada* s. str.) Statistics: L 1079, T 1, ci 24, ri 60. The single tree, in summary form, is shown as Cladogram 5.

In Cladograms 1 and 2 certain nodes are numbered, 1-39 in Cladograms 1a and 1b and 40-59 in Cladograms 2a and 2b.

Analysis A: Of the trees derived from Analysis A, we present one (Cladogram 1a) in full detail because it is based on all the taxa and all the characters. As will be shown below, other analyses provide better phylogenetic hypotheses.

A striking feature of Cladograms 1a and 1b is the extensive resolution. The consensus tree (Cladogram 1b) shows few polytomies; that is, most of the topological features of Cladogram 1a are found in all the trees based on Analysis A. The polytomies in the consensus tree (which in all other respects, of course, is like Cladogram 1a in topology) are listed below; the genera included in the family-group taxa are listed in the section on Classificatory Results.

1. Within the Melittidae (Node 2), four groups form a polytomy: *Macropis*, *Dasypoda*, *Hesperapis*, and a common stem for *Melitta* and *Meganomia*.
2. Within the Megachilinae (above Node 7), a polytomy supports four branches: *Osmia*, *Hoplitis*, the Megachilini and the Anthidiini.
3. *Isomalopsis*, *Exomalopsis*, and the stem leading to all taxa above (Node 31) form a trichotomy. (See reanalysis by Silveira, 1993.)
4. Immediately above this trichotomy there is another consisting of *Ctenoplectra*, the Emphorini, and the (Eucerini + *Tarsalia*) + the Tapinotaspini (Nodes 33, etc.).
5. Within the Emphorini (node above 34) there is a trichotomy consisting of *Melitoma*, *Diadasia*, and *Diadasina* + *Ptilothrix*.
6. Within the Tapinotaspini (Node 37) there is a polytomy consisting of *Caenonomada*, *Monoeca*, *Paratetrapedia* + the subgenus *Arhysoceble*, and *Tapinotaspis* + the subgenus *Tapinorhina*.
7. *Eucerinoda*, the rest of the Eucerini, and *Tarsalia* (Ancylini) form a trichotomy (Node 38).
8. Within the subtribe Eucerina (node above 39) there is a trichotomy consisting of *Canephorula*, *Melissodes* + *Svastra*, and *Eucera* + *Peponapis*.

Items 3 and 4 in the above list are the only ones involving stems leading to other major taxa.

There are few uniquely derived characters supporting the major (lower) nodes of Cladogram 1; a strong exception is Character 131 (number of ovarioles or testicular tubules) in Node 5. It is not surprising that some of the nodes, especially those supported by few characters (e.g., 9, 17, 19, 27), are weak and for biological understanding should be collapsed on the basis of our study. Further study by Silveira (1993), however, supports some of these nodes.

The characters of Node 1 (the common stem) include two apomorphies of melittids and L-T bees together (27-1, 42-1). A discussion of these and other common characters of Melittidae and L-T bees was given by Michener and Greenberg, 1980. Characters 68-3 (pre-episternal ridge) and 100-1 (submarginal cells) are reductions that are reversed at various points on the tree. We do not believe that they represent the true course of evolution because regaining of lost structures (e.g., a wing vein, character 100) is unlikely. See subsequent analyses for discussion.

Characters of Node 3 include several features of the mouthparts (34-1, 35-1, 41-1, 45-1, 48-1, 51-1, 52-1, 53-2 and 56-1) that are characteristic of L-T bees and differentiate them from S-T bees. Although the node is strongly supported, for most of these characters there are scattered reversals, and all but 56 reverse at least once. *Ctenoplectra* is the only taxon that reverses several (seven of nine) of these characters, including 48-1 which is the hallmark of L-T bees. Characters 76-1 (hind coxal articulation) and 91-1 (shape of middle tibia of female) are also features of most L-T bees, with only one reversal *(Tapinotaspis)* for 76 and scattered reversals for 91. Characters 84-1 (basitibial plates) and 113-1 (prepygidial fimbria) represent losses at Node 3; the structures reappear again elsewhere on the tree. Regaining of lost structures is not evolutionarily likely.

Node 5 is strongly supported by character 40-1, which is reversed only in Node 23. Character 122-1 is reversed only within Nomadinae and in *Coelioxoides* and *Isepeolus*. Character 131-1, four ovarioles or testicular tubules instead of three as in Megachilidae and S-T bees, does not reverse although more than four (131-2) occur in most Nomadinae, in *Ericrocis* and in *Apis*. Character 105-2, a very short jugal lobe, is primarily a feature of parasitic bees. In the cladogram it is reversed in Nodes 19 and 21. We do not believe this represents a likely evolutionary pattern, although we know nothing of the function of the jugal lobe or why it should be small in parasitic bees. Character 126-2 (volsella) is a loss. The volsella reappears in Node 21, in the Osirini, in the Isepeolini, in *Coelioxoides*, and in some Nomadinae. Since reacquisition of a lost structure is improbable, we question the probability of this reappearance.

Node 7 (Megachilinae) is supported by Characters 1-1 (subantennal sutures) and 31-1 (dististipital process), found only in this subfamily, although neither is conspicuous or uniformly well developed. Character 7-1 (long labrum) appears also in *Neofidelia*, *Thyreus*, and some Nomadinae, although in the Apidae with a long labrum, it does not have the broad basal articulation to the clypeus found in Megachilinae, and is clearly independently evolved.

Node 8 (Nomadinae) is supported by Character 53-1, which represents reduction of the flabellum as is frequent in parasitic (and some other) taxa. Character 111-1 (shape of S6 of female) is unique for the Nomadinae. Character 131-2 (more than four follicles) occurs in all Nomadinae for which the character is known except some species of *Nomada*. The clades within the Nomadinae are considered in the discussion of Classificatory Results.

Node 9 is supported by Characters 23-2 and 30-1, which are reversed in scattered taxa. Character 127-1 (spatha present) should probably be in Node 5 since most Nomadinae that do not have reduced genitalia have a spatha. The spatha is lost in scattered taxa above Node 9.

Node 17 is best supported by Character 68-1 (pre-episternal internal ridge curving back to scrobe), but the ridge is reduced or lost in various taxa (mostly parasitic) and extends a short distance downward (68-0) in *Isepeolus*. This node is not strongly supported.

Most of the remaining numbered nodes, likewise, are supported principally by characters that are weak because of repeated reversals and appearance of the same states also elsewhere in the tree. The following are the node numbers, each followed by a dash and numbers of character states that are infrequently reversed or repeated elsewhere in the study and therefore appear to give the stronger support for each: 18–50-1, 79-1; 19–89-1; 20–54-1, 74-1; 21–104-1; 23–90-1, reversal 40-0; 24–101-1, reversals 80-0, 91-0; 26–reversals 5-0, 75-0; 30–89-2; 31–62-1, 70-1, 79-1, 121-2, reversal 80-0; 33–58-1; 35-90-1; 36–63-1, reversal 6-0; 37–32-1, 72-1. Particularly weak nodes are 17, 18, 19, 21, 27, 30, 32, and 35.

The following are comments on strengths or weaknesses of the other numbered nodes.

Node 22 is supported especially by Character 106-2 (long, oblique vein cu-v of hind wing), which is found only here, although a less extreme version (106-1) occurs in some Anthophorini and in *Rhathymus*. Character 41-2 also appears in Anthophorini. Character 101-1 also appears in Anthophorini and elsewhere. Character 102-1 also appears in *Anthophora* and *Centris*, as well as elsewhere. Character 123-2 occurs also in *Epicharis*, some Osirini, and some Nomadinae. None of these characters seems related to the parasitism of the Ericrocidini and Melectini.

Node 25 (the apine clade) is one of the best-supported nodes in the study. Character 60-1 (expanded pollex) is unique except for the very different sort of expansion in Megachilinae. Character 85-1 (tibial corbicula) occurs elsewhere only in *Canephorula*. Other characters having to do with pollen manipulation and transport, Characters 86-1, 87-1, and 88-1, are unique to this node except that 87-1 occurs also in *Ctenoplectra* and 88-1 is reversed in Meliponini. Character 74-2 occurs also in some Melectini and Ericrocidini. Character 78-1, otherwise unknown in L-T bees, is reversed in Meliponini. Thus this node is supported not only by the well-known hind tibial characters but also by other features. Character 105-3 (loss of the jugal lobe), however, is reversed to 105-0 in *Apis* and Meliponini. Reappearance of lost structures is improbable and this reversal is evolutionarily unlikely; independent losses in Euglossini and *Bombus* involve the same number of steps as one loss and one gain and would be more likely.

Node 27 seems supported by Character 29-1 (stipital comb). This character, however, appears also at Node 23 and in most Osirini. Moreover, some Nomadinae have stipital concavities; they are probably derived from ancestors with the comb. Probably 29-1 should be at Node 5, as a character of Apidae, lost in numerous parasitic taxa. If this were done, Node 27 would have little support.

Node 28 has four reversals (6-0, 8-0, 23-0, and 30-0) of characters that appeared in Nodes 5 and 9. This supports the movement of the Xylocopinae toward the base of the tree as in Cladograms 2, 3, and 5, eliminating the reversals. Character 120-2 is found elsewhere only in *Apis*, where it looks very different.

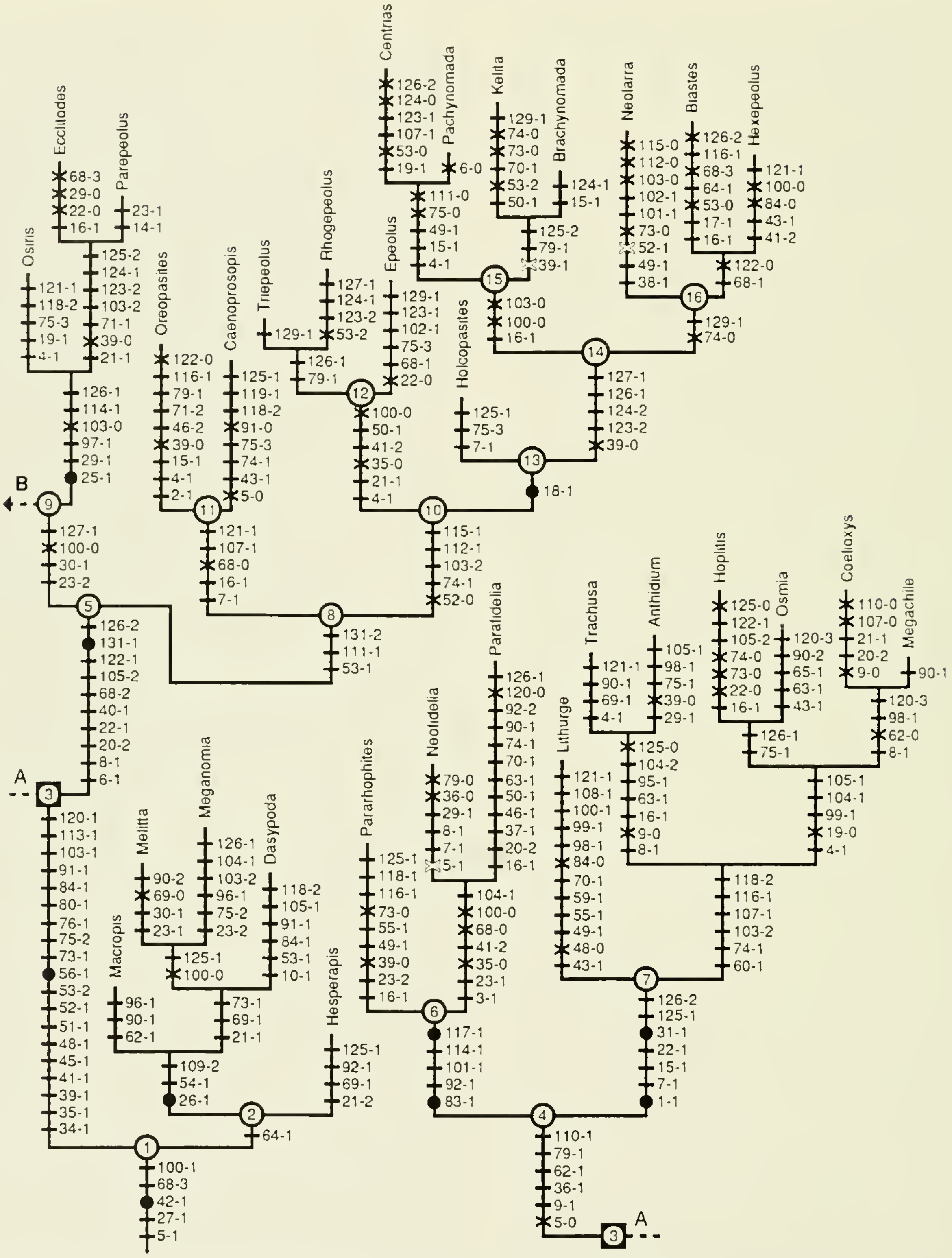
Node 29 is supported by Characters 3-2 (facial foveae) and 49-1 (incised base of labial palpus), which reverse to 3-1 and 49-0 in Node 33 and thus characterize the Exomalopsini. Moreover Character 75-1 is a reversal from 75-2, and goes back to 75-2 in Node 33. For further consideration of the Exomalopsini, see Silveira (1993).

Node 32 is supported by Character 19-1 which, however, appears in many other parasitic groups, but not in pollen-collecting bees. It is probably a convergent feature of parasitism rather than an indication of phyletic relationship. The other characters on this node are weak; the node itself should probably be eliminated in favor of a polytomy at Node 19.

Node 34 (Emphorini) is supported by Character 67-1, which is unique to the Emphorini. Character 11-1 (internal antennal sclerite) appears elsewhere in *Coelioxoides* and is only partly developed in *Ancyloscelis*.

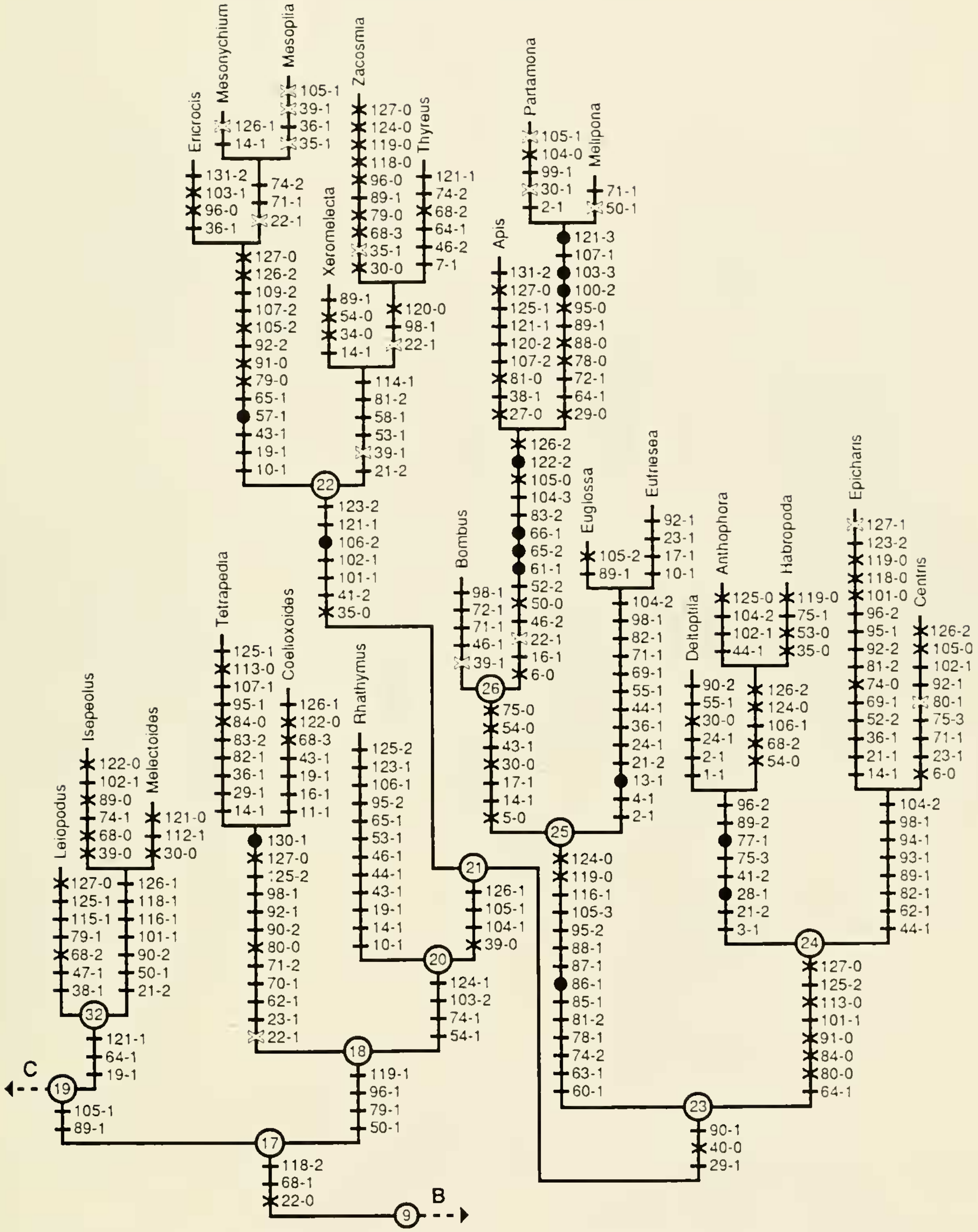
Node 38 (Eucerini + *Tarsalia*) is supported by Character 124-2, which appears also in Allodapini and Nomadinae but is so different as to be a good eucerine + ancyline character.

Node 39 (Eucerini) is supported by Character 12-1, which is unique for this group.



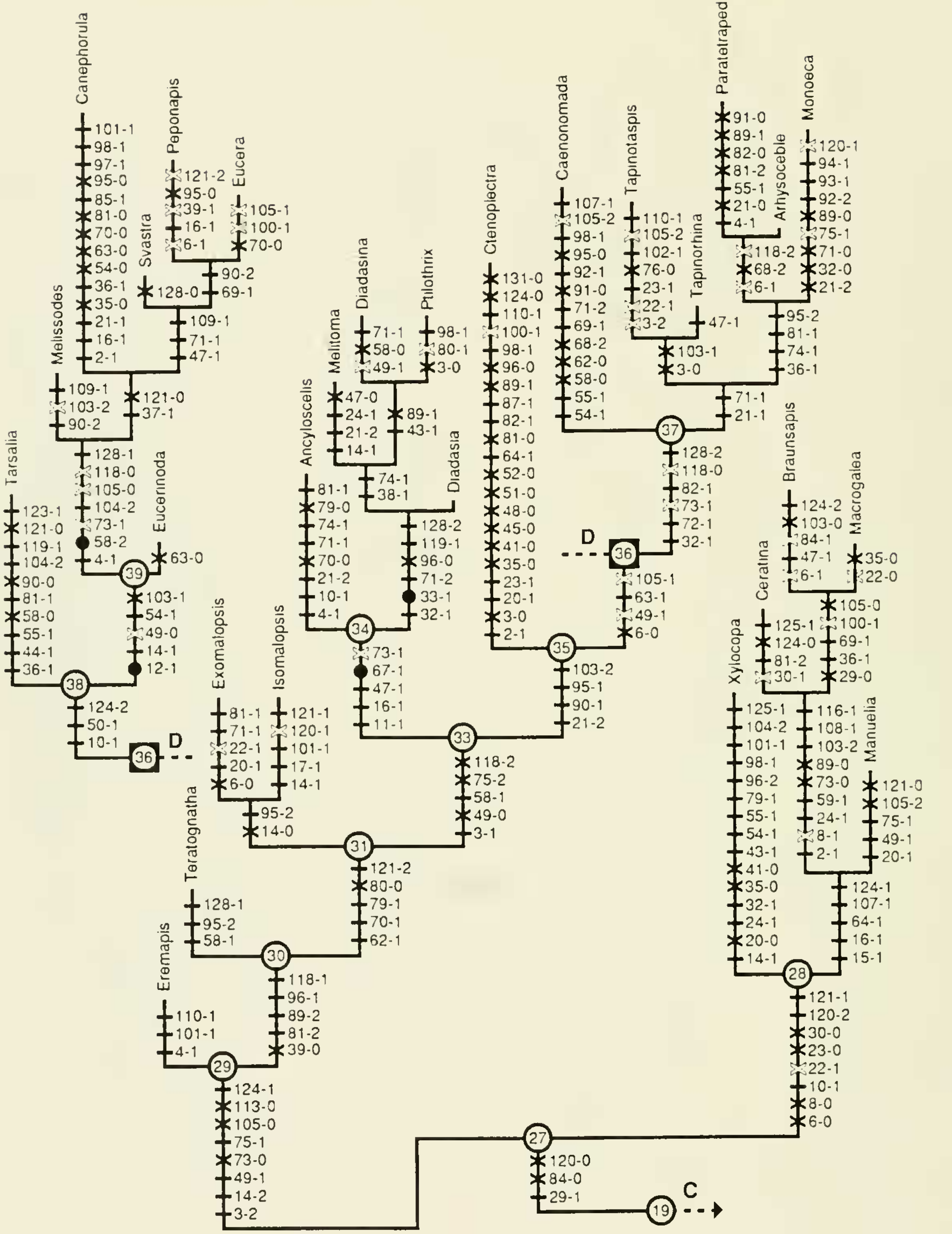
Cladogram 1a. One minimum-length tree based on Analysis A showing relationships based on adult characters among representative genera of long-tongued bees. The base of the cladogram is at the lower left of the first page. Characters are numbered according to the Annotated List of Adult Characters. Character transformation is symbolized as follows: dots indicate changes that occur

→



once in the tree, bars indicate changes that also occur in parallel elsewhere in the tree, black crosses indicate reversals to a state already present basally in the tree, white crosses indicate re-reversals. Only nodes referred to in the text are numbered. Capital letters and arrows indicate continuation of the tree on another page. Capital letters and black squares serve to match branches of the tree in the same page. Node 2 subtends the Melittidae; 4, the Megachilidae; 8, the Nomadinae; 25, the apine clade; and 28, the Xylocopinae.

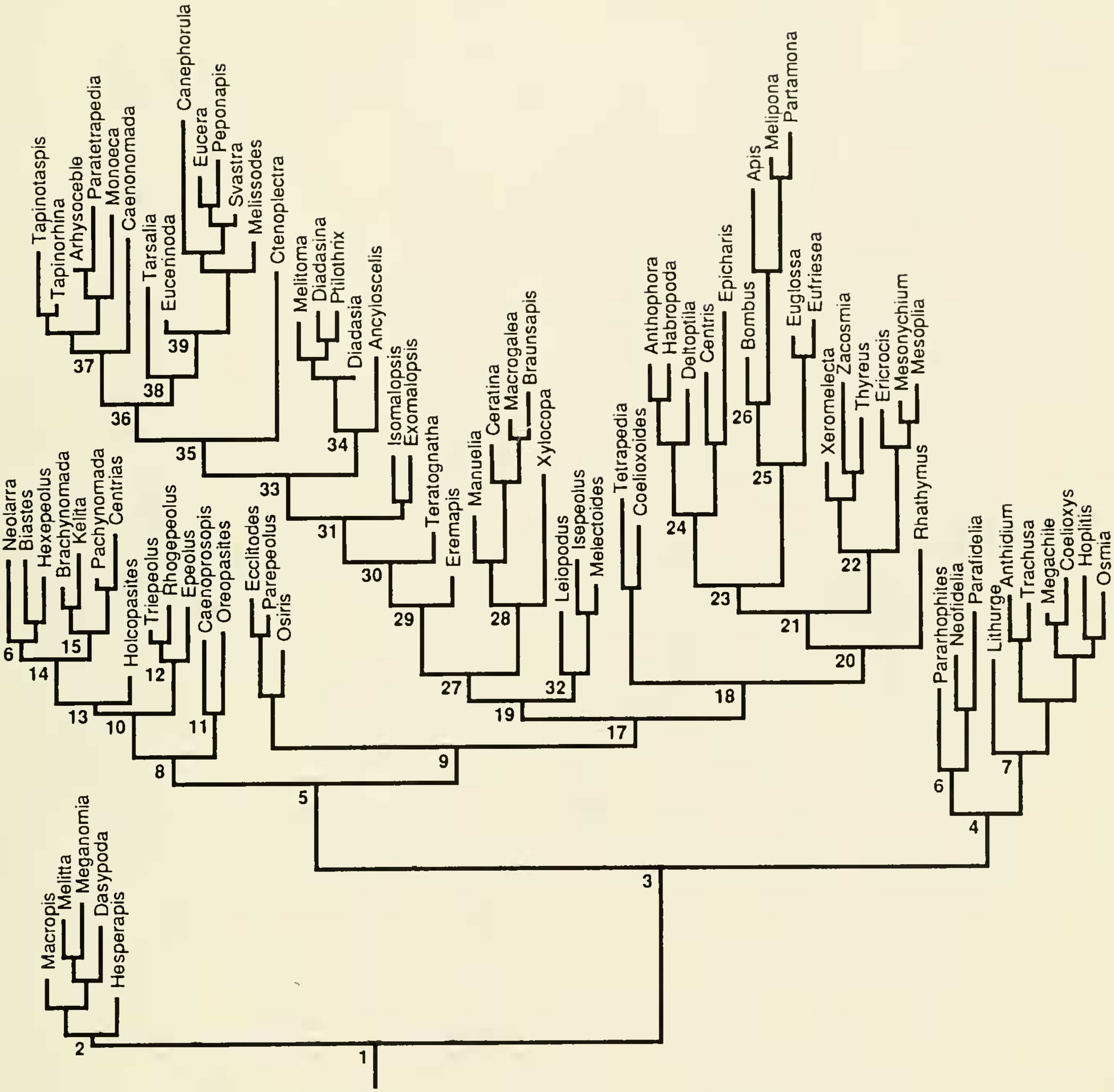
Continued on page 148



Cladogram 1a, continued.

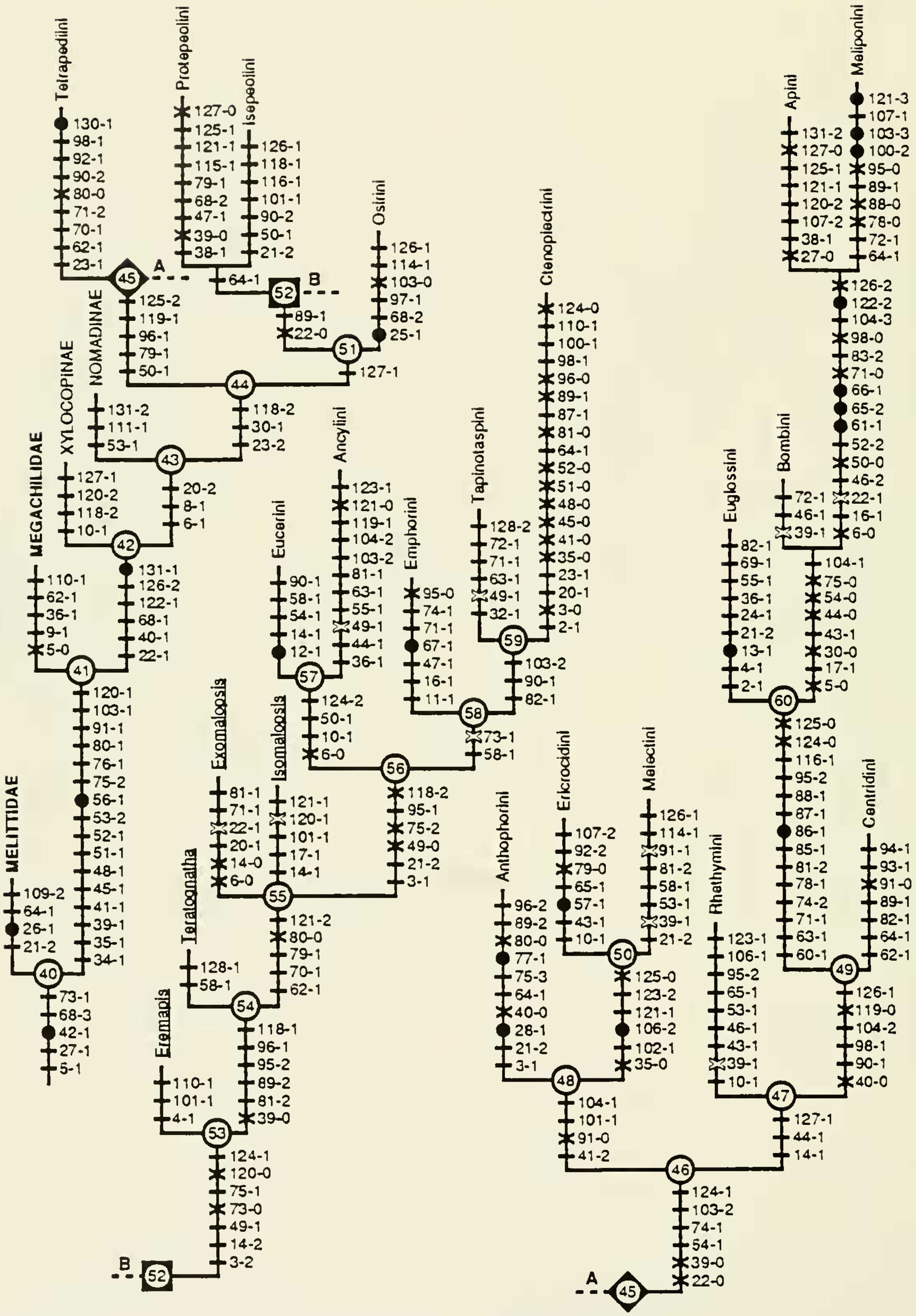
Analysis B: As explained above, this analysis contributed nothing of importance to our understanding of phylogeny since the trees produced were very similar to those of Analysis A. On the other hand, Analysis B added to our confidence since we could examine all the shortest trees. The fact that they were similar to the subset examined in Analysis A provides important support for this analysis.

In Analysis B the number of submarginal cells (Character 100) does not reverse from two to three, as in Analysis A.

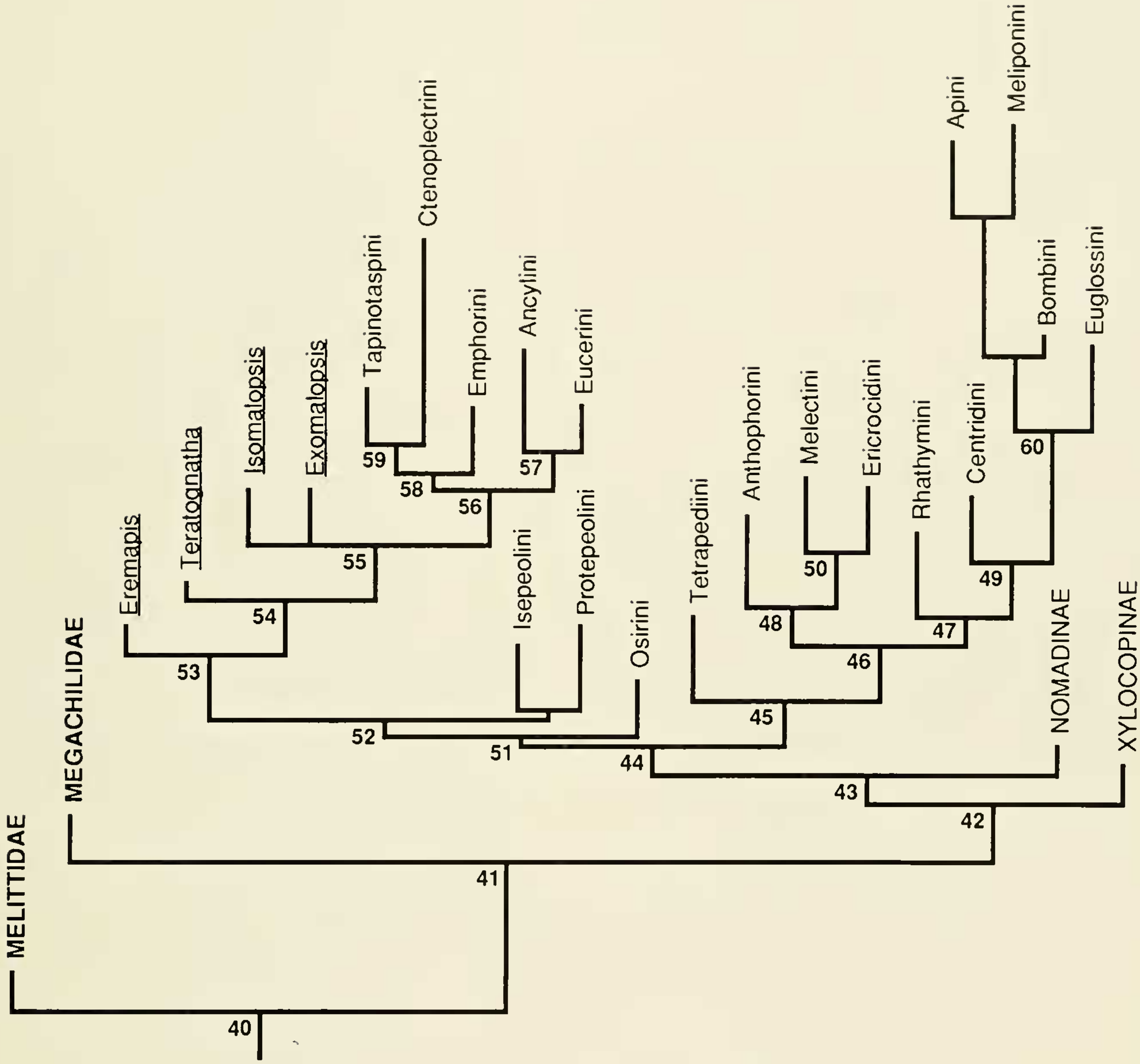


Cladogram 1b. Summary of Cladogram 1a with characters omitted. Lengths of vertical lines are proportional to the numbers of characters.

Analysis C: (Note that node numbers 1-39 are for Analysis A, Cladograms 1a, 1b, while numbers 40-60 are for Analysis C, Cladogram 2a, 2b.) Cladogram 2a, based on Analysis C (five characters associated with parasitism omitted), gives some striking rearrangements relative to Analysis A. There are no longer characters of parasites in the stem from which nonparasitic taxa seem to be derived. The Xylocopinae become the first branch of the Apidae, between Megachilidae and Nomadinae. In connection with this, Node 42 is supported by Characters 40-1, 68-1, 122-1, and 131-1. Character 126-2 (loss of volsella) is reversed higher in the cladogram, which is not evolutionarily likely. The support of the Xylocopinae lacks four reversals shown in Node 28 of Cladogram 1a; these characters appear in Nodes 43



Cladogram 2a. Basal parts (to families, subfamilies, and tribes) of tree based on adult characters, Analysis C (five characters related to parasitism omitted). The base of the cladogram is at the left.



Cladogram 2b. Summary of Cladogram 2a, as consensus tree. Lengths of vertical lines are proportional to the number of characters.

and 44. These nodes are supported by characters that were reasonably strong in Analysis A.

Node 45 is essentially like Node 18. Also the Tetrapediini is supported by largely the same characters in Analyses A and B but Nodes 46 and above are substantially rearranged. The Anthophorini and Centridini are dissociated, the latter becoming the sister group of the apine group of tribes. The consensus tree (Cladogram 2b) shows a polytomy of four branches: (a) Centridini + the apine clades, (b) Anthophorini, (c) Rhathymini, and (d) Melectini + Ericrocidini.

Node 51 is supported only by Character 127-1 (spatha). As noted in Analysis A, this feature appears in branches throughout the Apidae and should probably be in Node 42, with losses in certain taxa. Thus 127-1 is probably plesiomorphic for Apidae; if so, Node 51 would collapse.

Node 52 is supported by Character 89-1 which, however, appears also in Centridini and as 89-2 in Anthophorini.

The Protepeolini (*Leiopodus* in Cladogram 1a, 1b) and Isepeolini are united only by Character 64-1 (prosternal arms). A polytomy at 52 is a likely conservative interpretation.

The positions of *Eremapis* and *Teratognatha* are supported by Nodes 53 and 54, which have almost the same sets of characters as 29 and 30, Cladogram 1a. Node 55 is identical to 31. *Isomalopsis* and *Exomalopsis* are united in some of the Analysis C trees as is shown in Cladogram 1a. See Silveira (1993) for reanalysis of the Exomalopsini.

The remainder of Cladogram 2a is rather different from Cladogram 1a and the topology of different versions is diverse. The consensus tree shows a five-part polytomy as follows: (a) Ancylini (*Tarsalia* in Cladograms 1a and 1b), (b) Ctenoplectrini, (c) Tapinotaspini, (d) Emphorini, and (e) Eucerini. As in Cladograms 1a and 1b, *Canephorula* is in the midst of Eucerini, not a basal branch. Of the three topologies for this part of the cladogram found in Analysis C, one is shown in Cladogram 2a and 2b; another is as in Cladograms 1a and 1b. A third shows the following arrangement: ((((Ctenoplectrini, Tapinotaspini) Eucerini) Emphorini) Ancylini).

Analysis D: For this analysis (parasitic taxa excluded), a summary based on the consensus tree is presented as Cladogram 3a. Compared to Cladograms 1 and 2, various similarities are apparent. The Megachilidae are monophyletic and almost identical. The Xylocopinae are positioned as in Cladograms 2a and 2b and identical in branching pattern. (See the reanalysis of the Xylocopinae in the discussion of Classificatory Results.) As in Analyses A, B and C, the Exomalopsini constitute a paraphyletic group with the taxa arranged in the same way. (See the reanalysis by Silveira, 1993.) This group is located, however, between the Xylocopinae and all other Apinae, which are based on a large polytomy. In Analyses A, B and C there are two major branches separated at nodes 17 and 44 (see Cladograms 1 and 2). Such branches are not evident in Cladogram 3a, or in the individual trees upon which the consensus tree was based. The eight branches of the large polytomy in the consensus tree are as follows: (a) *Tetrapedia*, (b) *Tarsalia*, (c) *Eucerinoda*, (d) *Ctenoplectra*, (e) Tapinotaspini, (f) Emphorini, (g) Eucerina, and (h) a branch including Anthophorini, Centridini, and the apine clade. Thus a feature of Cladogram 3a is the association of the taxa listed under (h), as in Cladograms 1a and 1b.

With successive approximations character weighting by F. Silveira, all eight trees were alike in topology except for differences within the Melittidae and in the relative positions of *Isomalopsis*, *Exomalopsis*, and the stem leading to most other Apinae. The consensus tree is therefore completely resolved for L-T bees except for one polytomy. The topology for the Megachilidae, Xylocopinae, *Eremapis*, *Teratognatha*, and the polytomy (*Exomalopsis*, *Isomalopsis*, other Apinae) is as in Cladogram 3a. The other Apinae are divided into two main branches, as in Cladograms 1a, 1b, 2a, and 2b; unlike those cladograms, however, the Eucerini are in the same major branch as the apine clade and the Anthophorini, although near the base of this group and thus near the other branch. The topology for the Apinae above the polytomy is shown as light lines, Cladogram 3b.

Analysis E: Based on larvae, this analysis results in two islands of trees; the major one (176 trees) is summarized by a consensus tree, Cladogram 4. The minor island's consensus tree (based on 16 trees) is discussed below. In bees, larvae that spin cocoons are usually different in labial and other characters from larvae that have lost cocoon-spinning behavior. However, within L-T bees these differences do not appear to influence the tree greatly, for most L-T bees spin cocoons. Characters 43-2, 47-0, 49-1, 50-2, and 51-1 tend to appear among non-cocoon-spinning taxa; such taxa among L-T bees are *Thyreus*, *Epicharis*, Anthophorini, Xylocopinae, and Nomadinae, as well as one group of Melittidae.

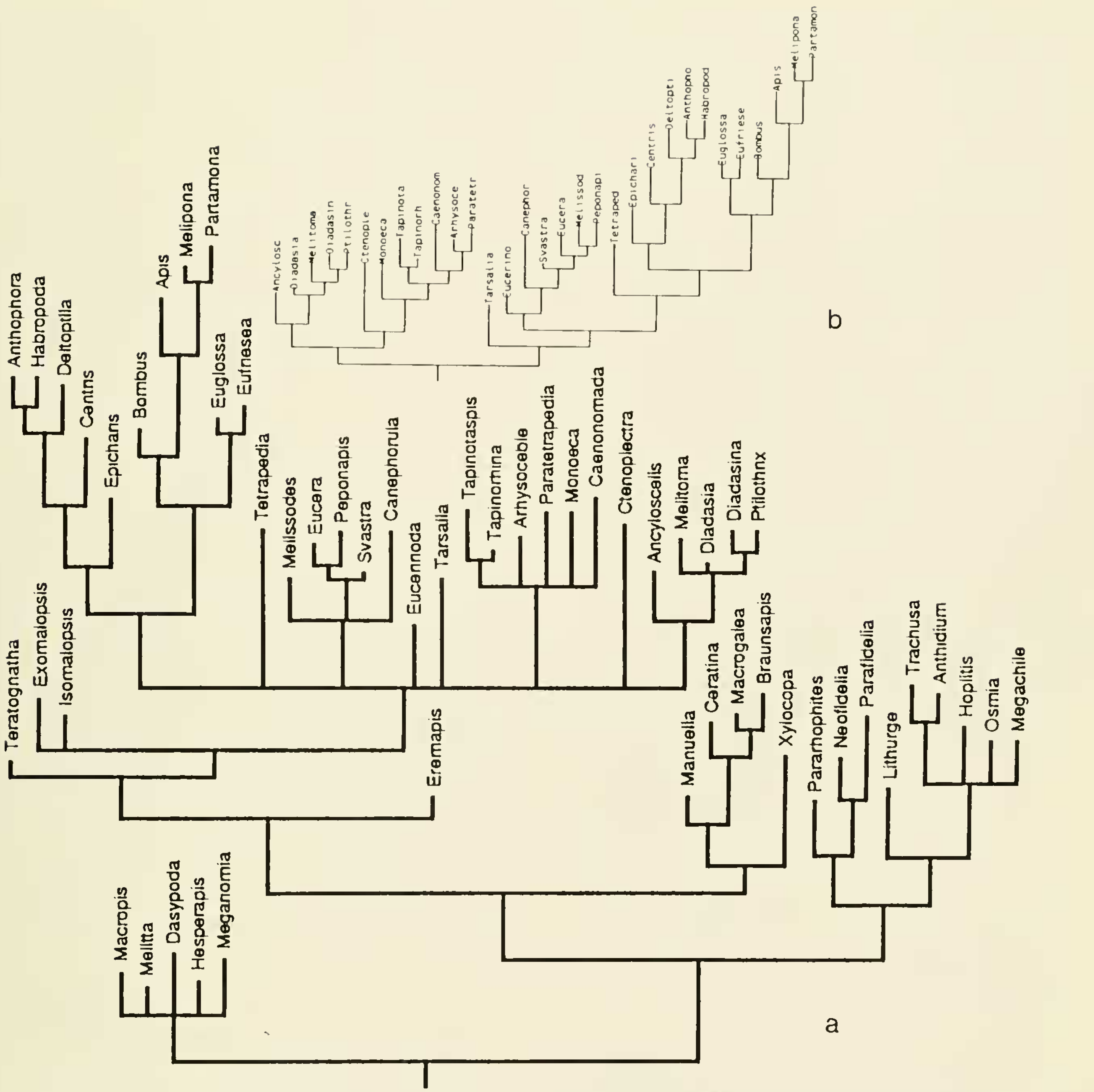
In the consensus tree for the major island of trees, the Nomadinae with *Isepeolus* form a clade. The Brachynomadini is the basal nomadine group in the consensus tree, in the trees of the minor island, and in Rozen, Eickwort and Eickwort's (1978) cladogram based on larvae. Also Neolarrini and Biastini are sister groups in these three analyses as are *Epeolus* and *Triepeolus*. Otherwise the three cladograms are quite dissimilar. We do not wish to support the paraphyly of Ammobatini indicated in Cladogram 4 as well as in the analysis of the minor island of trees.

The rest of the taxa in the consensus tree for the major island arise from a large polytomy (6 branches) as shown in Cladogram 4. One member of this polytomy contains *Rhathymus*, the Ericrocidini, Melectini, Ctenoplectrini, Megachilidae and the tribes of the apine clade. Within this large group, the most surprising subgroup consists of the apine complex and most Megachilidae, with the Megachilidae as a whole being a paraphyletic unit from which the apine complex arose. Since we did not directly examine the larvae, but merely used a table of characters, we only present this strange result, which disappears when larval and adult characters are used together (Analysis H, Cladogram 5).

The minor island of trees gives strange results that we find not useful. The Nomadinae are the sister group of *Dasypoda* in the Melittidae. In the consensus tree there is a trichotomy consisting of *Capicola*, *Hesperapis*, and *Dasypoda* + Nomadinae. This trichotomy is the sister group of all the other bees in our study, which are divided into two groups. One consists of *Exomalopsis*, *Paratetrapedia*, the Eucerina, Emphorina (the last two as sisters), the Anthophorini, Centridini, *Leiopodus*, the last as the sister to Xylocopinae. The other consists of the rest of the Melittidae, *Isepeolus*, the Melectini, Ericrocidini, *Ctenoplectra*, and the Megachilidae plus the tribes of the apine clade, the last arranged as in Cladogram 4.

Analyses F and G: These analyses were designed to compare phylogenies based on larvae (F) and on adults (G). Many of the groups were alike in the two analyses, but the connections (i.e., the relationships of major groups) were often quite different. Comparing the consensus trees, the following taxa or groups appear in both:

1. Megachilidae. For adults the arrangement is similar to that of Analysis A. For larvae, Megachilidae are the sister group to the apine clade and most genera form a polytomy except that *Neofidelia* and *Parafidelia* form a sister group arising from the polytomy.



Cladogram 3: a. Consensus tree based on adult characters, Analysis D (all cleptoparasitic taxa omitted). Lengths of vertical lines are proportional to numbers of characters. **b.** The same, large polytomy of 3a, resolved by use of successive approximations character weighting. (This is a consensus tree; polytomies occurred elsewhere.) The generic names are written out in full in Cladogram 3a.

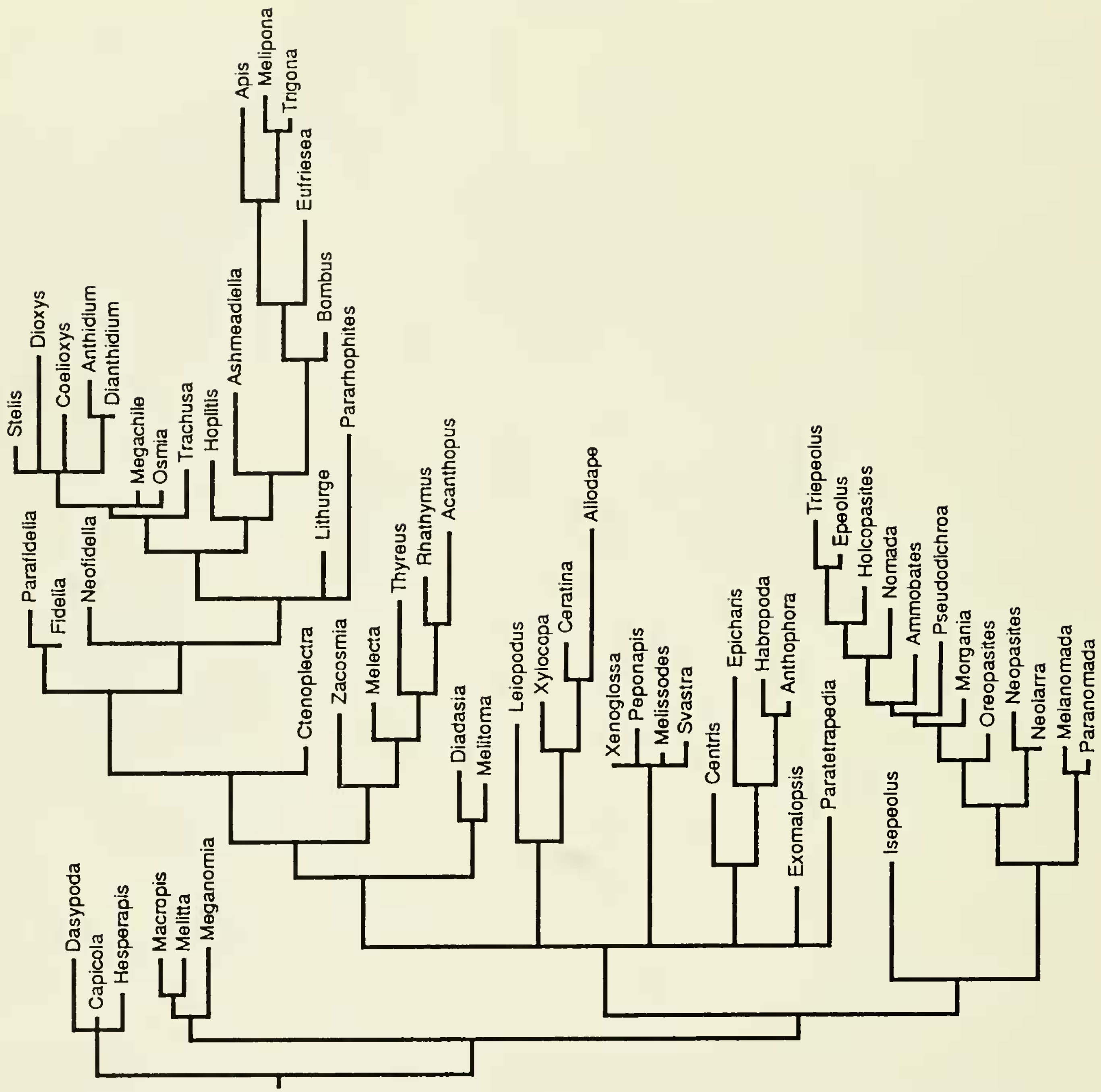
2. Nomadinae.

3. Xylocopinae. For adults the Xylocopinae is part of the large polytomy including all L-T bees except Megachilidae and Nomadinae. For larvae the Xylocopinae plus *Leiopodus* constitute the sister group to *Exomalopsis* + Emphorini + Eucerini.

4. Anthophorini—Centridini. For adults these tribes, as sisters, arise from the large polytomy. For larvae these tribes constitute the sister group to Xylocopinae + *Leiopodus* + *Exomalopsis* + Emphorini + Eucerini, and the Anthophorini arise from a paraphyletic Centridini.

5. The apine clade. For adults this clade arises from the large polytomy, *Bombus*, *Eufriesea*, and the rest forming a trichotomy. For larvae, this clade is the sister group of Megachilidae; *Bombus* is the first branch, *Eufriesea* the next.

6. Emphorini. For adults, part of a polytomy including *Exomalopsis*, *Paratetrapedia*, and Eucerini. For larvae, the sister group to Eucerini.



Cladogram 4. Consensus tree based on the larger island of minimum-length trees using larval characters, Analysis E. Lengths of vertical lines are proportional to numbers of characters.

7. Eucerini. See comments on Emphorini.

For adults, the Apidae are the sister group to Megachilidae, the two families together constituting the L-T bees. For larvae, the megachilids are a subgroup within the other L-T bees and sister group to the apine clade. But at the subfamily and tribal levels most genera fall within the same taxa (1-7 above) whether larvae or adult characters are used. The exceptions are eight genera. Two that clearly constitute the Melectini (*Zacosmia* and *Thyreus*) in the adult cladogram are not widely separated in that for larvae. The other six seem to occupy quite unrelated positions when one compares the trees based on larvae and on adults. They are *Ctenoplectra*, *Exomalopsis*, *Isepeolus*, *Leiopodus*, *Paratetrapedia* and *Rhathymus*. Each of these lacks close relatives available as both larvae and adults for our study; they are thus not closely related to other taxa in Analysis H.

From the above comments it is apparent that while the smaller groups (largely subfamilies and tribes, but including Megachilidae) usually are found in both the larval and adult cladograms, the arrangement of these groups is in some cases very different. Thus while larval characters usually support adult-based smaller groups, they do not always support the larger groups based on adult characters.

Analysis H: This analysis was based on larvae and adults combined, using the united matrices for Analyses F and G; it resulted in the single minimum-length tree shown in Cladogram 5. In a few features it is similar to the cladogram based on larval characters (Cladogram 4), but in other respects it resembles those based on adults. The following are interesting features of Cladogram 5.

1. Melittidae. As in the larval analysis (Cladogram 4), the melittids are divided and paraphyletic.

2. Megachilidae. This family is not associated with Apini and its relatives, as in the larval analysis, but within the family the Fideliinae is paraphyletic, in contrast to Analyses A-D and G, Cladograms 1-3. Moreover, *Hoplitis* and *Osmia* are separated rather than being sister groups as in Analysis A (Cladograms 1a and 1b).

3. Nomadinae. The included tribes are not arranged as in the other analyses. See the reanalysis under Classificatory Results.

4. *Isepeolus* and *Leiopodus* are separated, but as in Cladograms 1a, 1b, 2a, and 2b, appear near the base of the Apinae.

5. There are not two major branches such as separate at Nodes 17 and 44, Cladograms 1a, 1b, 2a, and 2b. The tribes of the apine complex are arranged as in Cladograms 1a and 1b but are not closely associated with Anthophorini or Centridini.

6. As in Cladograms 3a and 3b, *Centris* and *Epicharis* form a paraphyletic group from which the Anthophorini arose, instead of being a sister group to Anthophorini as in Cladograms 1a, 1b, 2a, and 2b.

7. *Exomalopsis* and *Paratetrapedia* are sister groups, together the sister group to Emphorini + Eucerini, this whole complex being the sister group to *Ctenoplectra*.

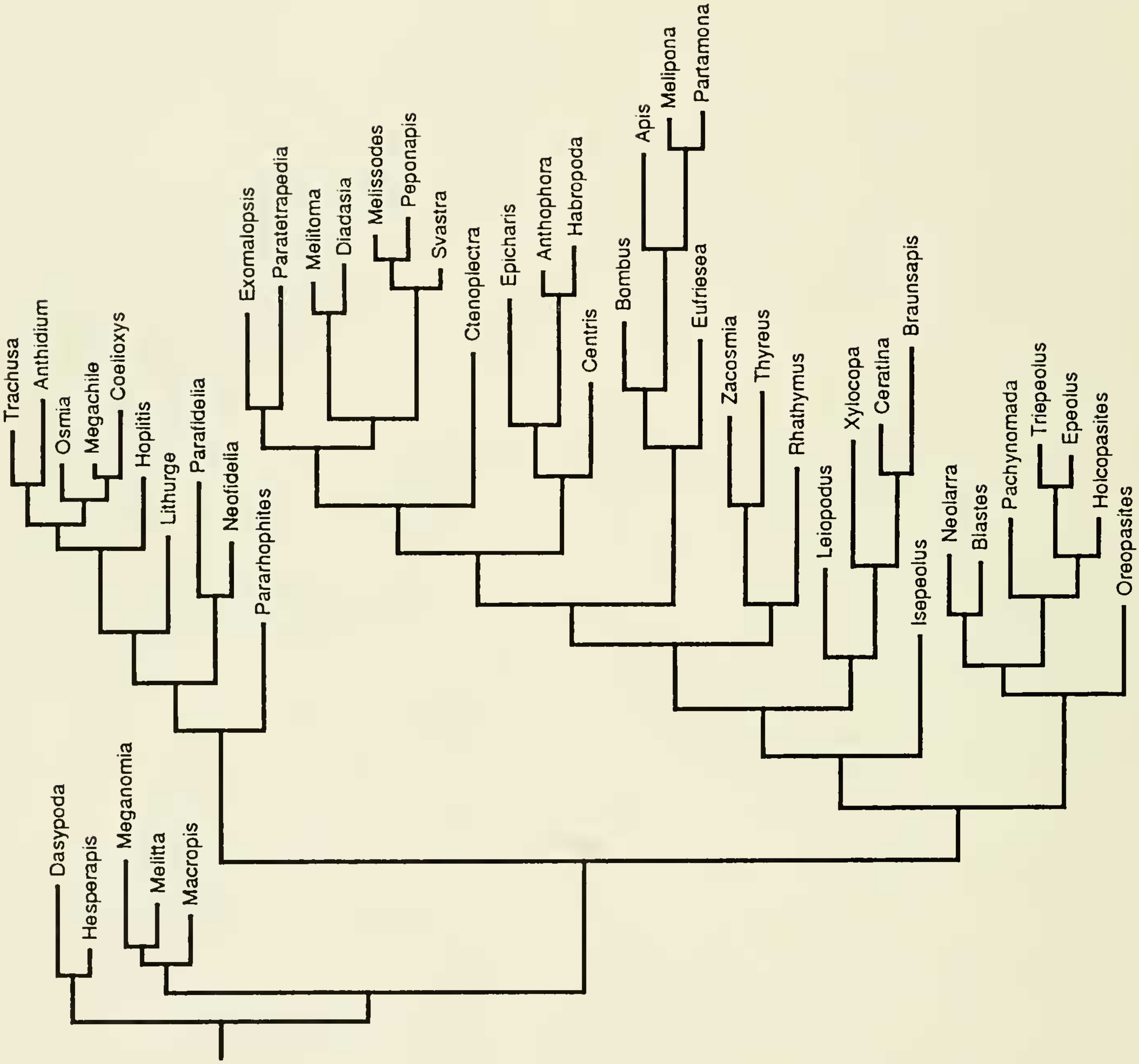
Many of the deviations from Analyses A to C are a result of the limited number of taxa for which larval data are available. For example, *Exomalopsis* cannot appear near other genera of Exomalopsini because there are no larval data for the latter.

CLASSIFICATORY RESULTS

At least the classificatory levels, and often other features of classifications, are subjectively determined. No one of our trees can be used alone for developing a classification. Analysis A has the full complement of adult characters and available taxa but results in cladograms in which features of parasitic bees evolve into those of nonparasitic bees, among other problems. Analysis C partly corrected this problem and is probably our best tree on which to base a classification, although it suffers from collapsing of certain nodes as explained for Analysis B in the preceding section. Analysis D, performed to further clarify the problems arising from parasitic bees, lacks all parasitic taxa. All other analyses lack many taxa because of the sparse information on larvae.

The following classification, therefore, is based on available information from the various analyses. Except for the Exomalopsini, all family-group taxa are found to be monophyletic in several or all of our analyses. The only commonly accepted family-group taxon of L-T bees not included in our study for lack of specimens to dismember, the Townsendiellini, is included on the basis of another study (Roig-Alsina, 1991). The genera included in the study, and occasionally others for clarification (the latter in parentheses) are listed.

Megachilidae
  Fideliinae
    Pararhophitini—*Pararhophites*
    Fideliini—*(Fidelia)*, *Neofidelia*, *Parafidelia*
  Megachilinae
    Lithurgini—*Lithurge*
    Anthidiini—*Anthidium*, *(Dioxys)*, *Trachusa*
    Megachilini—*Coelioxys*, *Megachile*
    Osmiini—*Hoplitis*, *Osmia*
Apidae
  Xylocopinae
    Xylocopini—*Xylocopa*
    Manueliini—*Manuelia*
    Ceratinini—*Ceratina*
    Allodapini—*(Allodape)*, *Braunsapis*, *Macrogalea*
  Nomadinae
    Ammobatini—*Ammobates*, *Oreopasites*,
    Caenoprosopidini—*Caenoprosopis*
    Neolarrini—*Neolarra*
    Townsendiellini—*(Townsendiella)*
    Nomadini—*Nomada*, subgenera *Centrias* and *Pachynomada*
    Biastini—*Biastes*, *(Neopasites)*
    Hexepeolini—*Hexepeolus*
    Ammobatoidini—*(Ammobatoides)*, *Holcopasites*
    Brachynomadini—*Brachynomada*, *Kelita*, *Melanomada*
    Epeolini—*Epeolus*, *Rhogepeolus*, *Triepeolus*
  Apinae
    Tetrapediini—*Coelioxoides*, *Tetrapedia*
    Rhathymini—*Rhathymus*
    Euglossini—*Eufriesea*, *Euglossa*
    Bombini—*Bombus*
    Apini—*Apis*
    Meliponini—*Melipona*, *Partamona*, *(Trigona)*
    Centridini—*Centris*, *Epicharis*
    Anthophorini—*Anthophora*, *Deltoptila*, *Habropoda*
    Ericrocidini—*Eriocrocis*, *Mesonychium*, *Mesoplia*
    Melectini—*(Melecta)*, *Thyreus*, *Xeromelecta*, *Zacosmia*



Cladogram 5. Minimum-length tree based on larval and adult characters, Analysis II. Lengths of vertical lines are proportional to numbers of characters.

Osirini—*Ecclitodes, (Epeoloides), Osiris, Parepeolus*
Protepeolini—*Leiopodus*
Isepeolini—*Isepeolus, Melectoides*
Exomalopsini—*Eremapis, Exomalopsis, Isomalopsis, Teratognatha*
Ancylini—*(Ancyla), Tarsalia*
Eucerini
  Eucerinodina—*Eucerinoda*
  Eucerina—*Canephorula, Eucera, Melissodes, Peponapis*
Emphorini
  Ancyloscelina—*Ancyloscelis*
  Emphorina—*Diadasia, Diadasina, Melitoma, Ptilothrix*
Ctenoplectrini—*Ctenoplectra*

Tapinotaspini—*Caenonomada, Monoeca, Paratetrapedia* and subgenus *Arhysoceble, Tapinotaspis* and subgenus *Tapinorhina*

Our cladograms should not be used to develop a classification of Melittidae. We included melittid genera for our analyses as an outgroup. To develop a classification of that family, more genera, probably other characters, and outgroups among the S-T bees should be used. Larvae suggest that the family Melittidae is not monophyletic and Michener (1981) found no synapomorphies for the family. We, however, found the small intercalary sclerite between the cardo and stipes (Character 26-1) which appears to be a family level synapomorphy. The sclerite, however, is sometimes exceedingly small and inconspicuous.

The Fideliinae, with its subdivision into tribes Pararhophitini and Fideliini, appears in all trees based on Analyses A to D. This arrangement, although not previously formalized, is similar to that which Rozen (in McGinley and Rozen, 1987) envisioned. The Fideliinae is strongly supported by Characters 83-1, 92-1, 114-1 and 117-1, the first and last of which are unique to this subfamily. Another unique character of the subfamily is the cocoon mixed with sand previously ingested by the larva (McGinley and Rozen, 1987).

The position of *Lithurge* as the sister group of the rest of the Megachilinae appears in all trees based on Analyses A, D and H. Synapomorphies of the tribe Lithurgini are listed by Michener (1983). If one wishes to use the category subtribe, then the Lithurgini and Megachilini could be the two tribes of Megachilinae, the Megachilini being divided into the subtribes Anthidiina, Megachilina, and Osmiina, although in the consensus tree of Analysis A *Osmia* and *Hoplitis* arise separately from the same polytomy as the other two tribes. We prefer the classification shown above because there is no objective basis for changing the established recognition of Anthidiini, Megachilini and Osmiini as tribes.

The subfamily Xylocopinae appears as a recognizable group in all trees. Its position at the base of the Apidae is shown in Analyses C and D (Cladograms 2 and 3) and it is near the base (above Nomadinae) in Analysis H (Cladogram 5). The sister group relationship of Xylocopinae to the apine clade indicated by Sakagami and Michener (1987) is seemingly incorrect. As indicated at that time, it was based largely on the similar structure of S8 of the male, which is now recognized as a plesiomorphy. There are, however, behavioral characters such as food storage outside the larval cells that support the supposed relationship of Xylocopinae with the apine clade. We now believe these behavioral similarities to be convergent.

Within the Xylocopinae, our analyses show *Xylocopa* to be the first branch, while Sakagami and Michener (1987) found *Manuelia* to be in that position, i.e., their tree differed from ours in that *Manuelia* and *Xylocopa* exchanged positions. We therefore reanalyzed the Xylocopinae, using the 41 characters of the present study that vary among our exemplars of the subfamily, repolarized as necessary according to the condition found in Node 42, and seven additional characters used by Sakagami and Michener (1987, characters 6, 16, 21-23, 26, 27). The outgroup used was all plesiomorphies (all 0's). The result was two equally parsimonious trees (statistics: L 64, T 2, ci 82, ri 71). The difference between the two trees is in the positions of *Xylocopa* and *Manuelia*, one having the topology of Sakagami and Michener (1987), the other that of the present study. If one must choose, CDM favors *Manuelia* as sister group to the others because of the strong synapomorphy of S8 of the male for the other tribes, countered by a plesiomorphic S8 in *Manuelia* (Sakagami and Michener, 1987). (It should be noted that Figure 10 of Sakagami and Michener [1987] is inverted; the truncated spiculum is directed upward on the page.)

The relationships within the subfamily Nomadinae as shown in Analysis A (Cladograms 1, 1a) differ in several respects from those based on larvae and those given by Roig-Alsina (1991). A reanalysis was made of Nomadinae alone, using 36 adult characters from the present study repolarized as necessary according to the condition found in Node 43, and adding nine other characters used by Roig-Alsina (1991, characters 4-8, 10-13) but omitted from our study of L-T bees. *Biastes* was coded as plesiomorphic for Roig-Alsina's character 12 (degree of fusion of furcula) because of the plesiomorphy seen in its near relative, *Rhopalolemma*. A single shortest tree (L 114, T 1, ci 46, ri 56) was found. It is like that of Roig-Alsina (1991) in topology except that the positions of *Hexepeolus* and *Nomada* are reversed. This reanalyzed tree of Nomadinae is presumably more reliable than that shown in our cladograms.

Our trees and Roig-Alsina's based on adults show *Oreopasites* and *Caenoprosopis* as the sister group to the rest. We considered using this division to recognize two tribes, each with subtribes. The larvae do not at all support such tribes (see Analysis F and Rozen, Eickwort and Eickwort, 1978) and in the study by Roig-Alsina (1991) *Townsendiella* could be equally parsimoniously placed in either tribe. Furthermore, the detailed analysis by Alexander (1990) does not demonstrate the two major groups within the Nomadinae that we found. We therefore retain the numerous tribes of previous works, and for consistency add two new ones, the Hexepeolini (new family-group name for *Hexepeolus*) and the Brachynomadini (new family-group name for *Brachynomada, Kelita, Melanomada, Paranomada*, and *Triopasites*). The Brachynomadini is the melanomadine complex of Alexander (1990).

The reason for the great difference between our results and Alexander's may include the following: He included taxa that we do not believe are Nomadinae; if we are correct his group was not monophyletic. Moveover, on the basis of information then available, he considered the Exomalopsini to be the outgroup; his polarization of some characters would therefore have differed from ours.

The Tetrapediini includes both *Tetrapedia* and the parasitic genus *Coelioxoides* in Analyses A and C (Cladograms 1a, 1b). Thus the placement of *Coelioxoides* by Roig-Alsina (1990) is supported. The two genera are so different (*Coelioxoides* being parasitic), however, that they might well be placed in separate subtribes. Since each would include only one genus, such subtribes would serve little purpose.

In Analyses A and G the Anthophorini and Centridini are sister groups whereas in Analysis C they are widely separated, and in D to F and H Centridini appear as paraphyletic with Anthophorini as the sister group either to *Epicharis* (Analyses E, F, H) or to *Centris* (Analysis D). We prefer to regard the Anthophorini and Centridini as separate, probably monophyletic tribes (see, however, the cladograms of Silveira, 1993). The association of the three genera of Anthophorini in our study is consistent and we do not believe that the tribal name Habropodini used by Brooks (1988) is necessary.

The tribes of the apine clade are Euglossini, Bombini, Apini and Meliponini. One of us (AR-A) would prefer to regard these as subtribes of a tribe Apini, to show their relationship to one another. The other (CDM) argues that the great differences among the four taxa justify recognition of each at the tribal level.

The many common characters of the apine clade (Nodes 25, 60) have been used in the past to justify family status. Michener (1944), however, united the Apidae and Anthophoridae under the former name; we support this conclusion, although Michener (1965) later recognized the families as separate. Those who would recognize a paraphyletic Anthophoridae from which Apidae arose must demonstrate a major gap in morphology between the two. In view of the strength of Nodes 25 and 60, this is surprisingly hard to do when both sexes, both female castes, and all included taxa are considered.

The arrangement of the four tribes of the apine clade is the same for Analyses A, C, D, and H (Cladograms 1, 2, 3, and 5). This is one of Michener's (1990c) two preferred arrangements; the other was a dichotomous arrangement (Michener's Figure 1) which is not supported by our study. Our arrangement is also the same as that proposed by Prentice (1991).

There is no morphological support for the sister group relationship of Bombini and Meliponini proposed by Cameron (1991) on the basis of mitochondrial DNA sequences and by Sheppard and McPherson (1991) on the basis of ribosomal DNA sequences.

The Ericrocidini and Melectini appear as sister groups in Analyses A and C (Cladograms 1 and 2). Since the common characters that indicate their relationship (see discussion of Node 22 above) are not obviously convergent features related to parasitic habits, these two tribes may be derived from a common parasitic ancestor.

The position of Osirini, Protepeolini, and Isepeolini well separated from the Nomadinae support the recent and sometimes tentative removal of these groups from Nomadinae or placement of them as basal branches in analyses of parasitic, *Nomada*-like bees (see Alexander, 1990; Roig-Alsina, 1991; and Rozen, Eickwort and Eickwort, 1978).

The Protepeolini *(Leiopodus)* appear in different positions in different trees. The association with Isepeolini in Cladograms 1 and 2 is weak. The larval characters indicate wide separation of the two tribes (Cladogram 4) and this is maintained in Cladogram 5. The modification of the metasomal apex associated with egg laying by parasites is so different as to suggest separate origins for the two tribes from nonparasitic ancestors. In any event, it seems best to separate Protepeolini and Isepeolini at the tribal level since the evidence for a sister group relationship is weak.

Protepeolus Linsley and Michener is a junior synonym of *Leiopodus* Smith (Roig-Alsina, new synonymy) but the tribal name is still Protepeolini.

The Exomalopsini in all cladograms based on adults appears to be a paraphyletic unit. In Analyses A and C this tribe seems far from the base of the Apinae. However, when one considers the small number and weakness of characters of Nodes 9, 17, 19, and 27 or 43, 44, 51, and 52, the Exomalopsini are seen to fall rather near the base of the Apinae. In Analysis D (Cladogram 3) they form the base of the large sister group to the Xylocopinae and thus constitute the base of the Apinae, a position not inconsistent with the larval information (Analysis E, Cladogram 4); larvae have not been described except for *Exomalopsis*. In Analysis H (Cladogram 5), however, *Exomalopsis* appears with *Paratetrapedia* in the Tapinotaspini as the sister group to Emphorini and Eucerini.

As noted above in the discussion of Analysis A, Node 29 is supported by three characters that appear in that node, characterize the Exomalopsini, and reverse in Node 33. Further analysis will probably reveal more characters with this distribution and show that the Exomalopsini is monophyletic. We recognize it as a tribe even if it is paraphyletic. Reanalysis by Silveira (1993) has provided better but not decisive evidence that it is monophyletic.

Taxa sometimes included in the Exomalopsini that are here shown to be distinct and not necessarily closely related to it are the Ancylini, the Tapinotaspini, and the genus *Ancyloscelis* in the Emphorini.

The Ancylini (*Ancyla* and *Tarsalia*, only the latter included in our study) appears in Cladograms 1a and 1b as the sister group to the Eucerini; in the consensus tree for Analysis A, it is in a polytomy with *Eucerinoda* and the other Eucerini. In Analysis C the consensus tree shows it in a polytomy with four other taxa, one of which is the Eucerini. In Analysis D the consensus tree places *Tarsalia*, *Eucerinoda*, other Eucerini, and five other taxa in a polytomy. Our impression was that Ancylini represents a basal branch of the eucerine clade but since the evidence was not clear, we maintained Ancylini as a tribe. Silveira (1993), however, has reexamined the data, added *Ancyla* to his analysis, and concluded that a sister-group relationship to the Eucerini is not likely.

The Eucerini appear consistently as a clade including as its basal branch the Chilean genus *Eucerinoda*. Larvae of the latter are unknown but larval characters group other Eucerini (Cladogram 4). *Eucerinoda* lacks various features of the previously recognized Eucerini including the long paraglossae, hitherto considered a unique feature of the tribe. We therefore recognize two subtribes, Eucerinodina and Eucerina, relegating the former Eucerinodini to subtribal status.

Canephorula falls easily within the Eucerina and therefore the tribe Canephorulini vanishes.

The genera of Emphorini are consistently grouped, with *Ancyloscelis* as sister to the others. Placement of *Ancyloscelis* in the Emphorini was suggested earlier by J. S. Moure (in litt.). It is different enough from other Emphorini that we propose subtribal status for it, the Ancyloscelina new subtribe, as distinguished from Emphorina.

The Ctenoplectrini, the remarkable features of which led to its recognition as a distinct family (e.g., Michener and Greenberg, 1980), is a tribe of Apinae. The characters that led Michener and Greenberg to place the Ctenoplectridae as the sister group to all L-T bees are now recognized as reversals in the mouthparts toward S-T bee characteristics (see Introduction; also Silveira, in press).

The Tapinotaspini is a new family-group name for a distinctive group of genera formerly included in Exomalopsini. These genera are those of sections 1, 2, and 5 of Exomalopsini as understood by Michener and Moure (1957); in that work the relationship of these three sections was recognized. The proposed relationships of *Caenonomada* to Centridini, Rhathymini and Ericrocidini (Snelling and Brooks, 1985) and of *Monoeca* to Centridini (Neff and Simpson, 1981) are not supported.

CONCLUDING REMARKS

Our work was based on exemplars of a limited list of genera. Familiarity with other species and other genera suggests to us that most of the character states that we recorded apply also to the relatives of each exemplar. But we know of cases in which this is not true for certain characters, and there are doubtless many more such cases. Each group needs to be more broadly examined to clarify such matters. Moreover, each group needs to be reanalyzed not only to include genera and species that we did not study in detail, but to re-evaluate the characters that we did use.

Among the difficulties in a study of a large group such as the L-T bees are selection of synapomorphic characters and coding of their states. One would bias the results unduly toward the prior classification by using only those characters already known to distinguish recognized taxa; in L-T bees another problem resulting from such a policy would be too few characters for a reasonable analysis. We therefore used as many polarizable characters as we could find that were not autapomorphic at the level of our exemplars. Many of these characters had low consistency indices, reversing and rereversing, or a given state appearing to have evolved repeatedly among diverse taxa. These characters, however, may be phylogenetically important within smaller groups, such as a tribe. Homologies can be more certainly appraised within such a group. For such a study the polarity of some characters may be altered relative to our study; our polarization was for L-T bees as a whole but for analysis of a smaller group such as a tribe, polarity should be determined on the basis of outgroups for that tribe. We hope our results will help in selecting such outgroups. Users of our work for this purpose should note, however, that certain nodes (we list the worst above) are weak: outgroups should be selected as though these nodes were polytomies even though they may be supported in consensus trees. When levels of homoplasy are high, as they were in this study, minimum-length trees based on parsimony may be extremely unstable in the face of additional characters or taxa, so that weak nodes should never be taken too seriously. As indicated in the section on Classificatory Results, we here report reanalyses, with additional characters and repolarizations as necessary, for the tribes of Xylocopinae and Nomadinae. Moreover Silveira (1993) has made such a reanalysis of the Apinae.

Some preliminary biogeographical comments based on the distributions of the 41 terminal suprageneric taxa of L-T bees are now possible. The numbers of such taxa in major biogeographical regions are as follows: neotropical 29, nearctic 25, palearctic 20, subsaharan Africa 17, oriental 16 and Australia including New Guinea 11. In general these numbers are correlated with the climatic and ecological diversity of the areas. The neotropical region has the greatest number of taxa. Its great importance for bee taxa is further shown by the fact that it is the area of maximum diversity for several widespread taxa: Lithurgini, Epeolini, and Meliponini. The neotropical region also has the greatest climatic diversity—tropical forest, savanna, southern temperate areas, mountains, deserts, etc. North America has great diversity but the North American tropics are placed in the neotropical region; if one excludes basically neotropical taxa that range into the southern nearctic, there are only 20 nearctic taxa.

Of greater interest are the possible contributions of distributional patterns to our knowledge of antiquity of taxa. Fourteen of the taxa are restricted to the neotropical region or are basically neotropical but extend north only into the southwestern nearctic region. Absence of these taxa from Africa suggests that they are probably of more recent origin than the full separation of South America and Africa; it was probably Eocene or later before the Atlantic was wide enough to form a long-term barrier for flying insects like bees.

Two pairs of tribes, each of which may owe its duality to the long isolation of South America after its separation from Africa, are the Anthophorini-Centridini and the Melectini-Ericrocidini. (The sister-group relationship of Anthophorini and Centridini is by no means certain.) In each case the first listed tribe is widely distributed but scarce or (for Melectini) absent in South America, while the second is principally South American, although ranging north in reduced diversity into the southwestern United States. These tribes are therefore likely to be younger than the separation of Africa and South America. These pairs are not independent; the Melectini are cleptoparasites of Anthophorini, the Ericrocidini, of Centridini.

The Fideliini, a relict group now found in desertic areas of southern Africa, with one species of *Fidelia* in Morocco and the genus *Neofidelia* in central Chile, may once have been widespread, or an old, limited distribution may have been divided by the spreading Atlantic Ocean.

The pantropical Meliponini, which occurred as far north as the Baltic region in late Eocene times and as New Jersey in late Cretaceous, probably owes its wide distribution to its antiquity. Nonetheless, no genera are the same on both sides of the Atlantic Ocean (Michener, 1990c) although *Trigona* occurs both in the neotropics and in the Indoaustralian region; the genera are probably more recent than the Atlantic.

For the majority of bee family-group taxa, fossil evidence is totally lacking. Fossils of Meliponini are mentioned above; for comments on the reliability of the late Cretaceous date for *Trigona*, see Rasnitsyn and Michener (1991). Otherwise, among L-T bees, the apine clade has well-preserved and identifiable fossil species as old as the Eocene (Zeuner and Manning, 1976); forms assigned to the Ctenoplectrini may be misplaced.

There is not even a tendency for old taxa (as judged by the fossil record) to be near the bases of the cladograms. Of course the fossil record is extremely fragmentary and biased toward taxa that collect resin for nesting purposes and thus occasionally are trapped in it and fossilized in amber. The fragmentary record that we have, however, and the fact that bee evolution may not have begun until the rise of the angiosperms in the early Cretaceous, suggest that there may have been a rapid early radiation, followed by relative stasis in some clades. Families well represented in Australia are S-T bees (Colletidae, Stenotritidae, and Halictidae) and the Colletinae show congeneric relationships to South American forms. Therefore the major radiation of S-T bees, at least the Colletinae, presumably preceded the interruption of the Australian-South American biotic exchange through Antarctica.

There are no family-group taxa of L-T bees limited to or highly diversified in Australia. Therefore L-T bees there are relatively recent arrivals, and L-T bees as a group must be more recent, at least in the southern hemisphere, than the time when Australia became isolated from other land masses. Thus the major early radiation of L-T bees either postdated that time or possibly was in other parts of the world.

Appendix: NUMBER OF TUBULES IN REPRODUCTIVE ORGANS

The number of ovarioles per ovary and of sperm tubules per testis (Character 131) is one of the strongest characters for separating families of L-T bees. Of course dissections have not been made for all genera; exceptions may yet be found. Based on the literature and our own dissections, the numbers are the same for ovaries and testes, and are three for S-T bees and megachilids, four for Apidae except that in *Apis* and some parasitic groups (Nomadinae, *Ericrocis*) there are even more. This statement is based in part on the literature (Alexander and Rozen, 1987; Iwata, 1955; Iwata and Sakagami, 1966; Rozen, 1986; Rozen and Roig-Alsina, 1991 and numerous works on halictid and allodapine bee life histories and social biology, in which ovarian development has been routinely examined, and number of ovarioles incidentally reported or illustrated; see citations in Michener, 1974, 1990a, b). In addition the results of new dissections are listed below:

Females, number of ovarioles per ovary: *Manuelia gayatina* (Spinola), 4; *Ancyloscelis apiformis* (Fabricius), 4.

Males, number of tubules per testis: *Hesperapis carinata* Stevens, 3; *Anthidium porterae* Cockerell, 3; *Megachile mendica* Cresson, 3; *Megachile petulans* Cresson, 3; *Xylocopa virginica* (Linnaeus), 4; *Ceratina calcarata* Robertson, 4; *Triepeolus distinctus* Cresson, 5; *Bombus pennsylvanicus* (DeGeer), 4; *Bombus bimaculatus* Cresson, 4; *Euglossa viridissima* Friese, 4; *Exomalopsis pygmaea* (Cresson), 4; *Paratetrapedia* sp., 4; *Ptilothrix bombiformis* (Cresson), 4; *Diadasia baeri* (Vachal), 4; *Melissodes agilis* Cresson, 4; *Svastra obliqua* (Say), 4; *Peponapis pruinosa* (Say), 4; *Anthophora walshii* Cresson, 4; *Habropoda pallida* (Timberlake), 4; *Centris atripes* Mocsáry, 4.

LITERATURE CITED

Alexander, B. 1990. A cladistic analysis of the nomadine bees. Systematic Entomology 15: 121-152.

Alexander, B., and J. G. Rozen, Jr. 1987. Ovaries, ovarioles and oocytes in parasitic bees. Pan-Pacific Entomologist 63: 155-164.

Ashmead, W. H. 1899. Classification of the bees, or the superfamily Apoidea. Transactions of the American Entomological Society 26: 49-100.

Börner, C. 1919. Stammesgeschichte der Hautflügler. Biologisches Zentralblatt 39: 145-186.

Brooks, R. W. 1988. Systematics and phylogeny of the anthophorine bees. University of Kansas Science Bulletin 53: 436-575.

Brothers, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. University of Kansas Science Bulletin 50: 483-649.

Cameron, S. 1991. A new tribal phylogeny of the Apidae inferred from mitochondrial DNA sequences. Pp. 71-87 *in* D. R. Smith (ed.), Diversity in the Genus *Apis*. Boulder, Colorado: Westview Press.

Cane, J. H. 1979. The hind tibiotarsal and tibial spur articulations in bees. Journal of the Kansas Entomological Society 52: 123-137.

Cresson, E. T. 1887. Synopsis of the families and genera of the Hymenoptera of America, north of Mexico. Transactions of the American Entomological Society, Suppl. Vol.: i-iv + 1-154.

Ehrenfeld, J., and J. G. Rozen, Jr. 1977. The cuckoo bee genus *Kelita*, its systematics, biology, and larvae. American Museum Novitates no. 2631: 1-24.

Farris, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

Farris, J. S. 1988. Hennig86: Version 1.5. Port Jefferson Station, N. Y.: distributed by the author.

Iwata, K. 1955. The comparative anatomy of the ovary in Hymenoptera. Part I. Aculeata. Mushi 29: 17-34.

Iwata, K., and S. F. Sakagami. 1966. Gigantism and dwarfism in bee eggs in relation to the modes of life, with notes on the number of ovarioles. Japanese Journal of Ecology 16: 4-16.

Jander, R. 1976. Grooming and pollen manipulation in bees (Apoidea): The nature and evolution of movements involving the foreleg. Physiological Entomology 1: 179-194.

Kirby, W. 1802. Monographia Apum Angliae. Vol. 1, xxii + 258 pp.; vol. 2, 338 pp. + 18 pls. Ipswich.

Laroca, S., C. D. Michener and R. M. Hofmeister. 1989. Long mouthparts among "short-tongued" bees and the fine structure of the labium in *Niltonia*. Journal of the Kansas Entomological Society 62: 400-410.

Latreille, P. A. 1802. Histoire Naturelle des Fourmis. xvi + 445 pp, 12 pls. Paris.

Lepeletier de Saint-Fargeau, A. 1836, 1841. Histoire Naturelle des Insectes—Hyménoptères. Vol. 1, 547 pp.; vol. 2, 680 pp. Paris.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Systematic Zoology 40: 315-328.

McGinley, R. J. 1981. Systematics of the Colletidae based on mature larvae with phenetic analysis of apoid larvae. University of California Publications in Entomology 91: i-xvi + 1-307.

McGinley, R. J., and J. G. Rozen, Jr. 1987. Nesting biology, immature states, and phylogenetic placement of the palearctic bee *Pararhophites*. American Museum Novitates no. 2903: 1-21.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees. Bulletin of the American Museum of Natural History 82: 151-326.

Michener, C. D. 1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. University of Kansas Science Bulletin 35: 987-1102.

Michener, C. D. 1965. A classification of the bees of the Australian and South Pacific regions. Bulletin of the American Museum of Natural History 130: 1-362, pls. 1-15.

Michener, C. D. 1970. Social parasites among African allodapine bees. Zoological Journal of the Linnean Society [London] 49: 199-215.

Michener, C. D. 1974. The Social Behavior of the Bees: A Comparative Study. i-xii + 1-404 pp. Cambridge, Massachusetts: Harvard University Press.

Michener, C. D. 1975. A taxonomic study of African allodapine bees. Bulletin of the American Museum of Natural History 155: 67-240.

Michener, C. D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66: 277-347.

Michener, C. D. 1981. Classification of the bee family Melittidae with a review of species of Meganomiinae. Contributions of the American Entomological Institute 18(3): i-iii + 1-135.

Michener, C. D. 1983. The classification of the Lithurginae. Pan-Pacific Entomologist 59: 176-187.

Michener, C. D. 1985. A comparative study of the mentum and lorum of bees. Journal of the Kansas Entomological Society 57(for 1984): 705-714.

Michener, C. D. 1990a. Reproduction and caste in social halictine bees. Pp. 77-121 *in* W. Engels (ed.), Social Insects—An Evolutionary Approach to Castes and Reproduction. Berlin: Springer-Verlag.

Michener, C. D. 1990b. Castes in xylocopine bees. Pp. 123-146 *in* W. Engels (ed.), Social Insects—An Evolutionary Approach to Castes and Reproduction. Berlin: Springer-Verlag.

Michener, C. D. 1990c. Classification of the Apidae. University of Kansas Science Bulletin 54: 75-164.

Michener, C. D., and R. W. Brooks. 1984. Comparative study of the glossae of bees. Contributions of the American Entomological Institute 22(1): i-iii + 1-73.

Michener, C. D., and A. Fraser. 1978. A comparative anatomical study of mandibular structure in bees. University of Kansas Science Bulletin 51: 463-482.

Michener, C. D., and L. Greenberg. 1980. Ctenoplectridae and the origin of long-tongued bees. Zoological Journal of the Linnean Society [London] 69: 183-203.

Michener, C. D., and J. S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees. Bulletin of the American Museum of Natural History 112: 395-451.

Neff, J. L., and B. B. Simpson. 1981. Oil-collecting structures in the Anthophoridae (Hymenoptera): Morphology, function, and use in systematics. Journal of the Kansas Entomological Society 54: 95-123.

Plant, J., and H. F. Paulus. 1987. Comparative morphology of the postmentum of bees (Hymenoptera: Apoidea) with special remarks on the evolution of the lorum. Zeitschrift fur Zoologische Systematik und Evolutionsforschung 25: 81-103.

Popov, V. V. 1949. Tribe Pararhophitini (Hymenoptera, Anthophorinae) as an early Tertiary element of the contemporary fauna of the desert in Central Asia and Egypt. Doklady Akademii Nauk SSSR 66: 507-510 [in Russian].

Prentice, M. 1991. Morphological analysis of the tribes of Apidae. Pp. 51-69 *in* D. R. Smith (ed.), Diversity in the Genus *Apis*. Boulder, Colorado: Westview Press.

Rasnitzyn, A. P., and C. D. Michener. 1991. Miocene fossil bumble bee from the Soviet far east with comments on the chronology and distribution of fossil bees. Annals of the Entomological Society of America 84: 583-589.

Robertson, C. 1904. Synopsis of Anthophila. Canadian Entomologist 36: 37-43.

Roig-Alsina, A. 1989. The tribe Osirini, its scope, classification, and revisions of the genera *Parepeolus* and *Osirinus*. University of Kansas Science Bulletin 54: 1-23.

Roig-Alsina, A. 1990. *Coelioxoides* Cresson, a parasitic genus of Tetrapediini. Journal of the Kansas Entomological Society 63: 279-287.

Roig-Alsina, A. 1991. Cladistic analyses of the Nomadinae s. str. with description of a new genus. Journal of the Kansas Entomological Society 64: 23-37.

Rozen, J. G., Jr. 1977. The ethology and systematic relationships of fideliine bees, including a description of the mature larva of *Parafidelia*. American Museum Novitates no. 2637: 1-15.

Rozen, J. R., Jr. 1986. Survey of the number of ovarioles in various taxa of bees. Proceedings of the Entomological Society of Washington 88: 707-710.

Rozen, J. R., Jr. 1987. Nesting biology of the bee *Ashmeadiella holtii* and its cleptoparasite, a new species of *Stelis*. American Museum Novitates no. 2900: 1-10.

Rozen, J. G., Jr. 1991. Biology and larvae of the cleptoparasitic bee *Townsendiella pulchra* and nesting biology of its host, *Hesperapis larreae*. American Museum Novitates no. 3005: 1-11.

Rozen, J. G., Jr., K. R. Eickwort and G. C. Eickwort. 1978. The bionomics and immature stages of the cleptoparasitic bee genus *Protepeolus*. American Museum Novitates no. 2640: 1-24.

Rozen, J. G., Jr., and C. D. Michener. 1988. Nests and immature stages of the bee *Paratetrapedia swainsonae*. American Museum Novitates no. 2909: 1-13.

Rozen, J. G., Jr., and A. Roig-Alsina. 1991. Biology, larvae, and oocytes of the parasitic bee tribe Caenoprosopidini. American Museum Novitates no. 3004: 1-10.

Sakagami, S. F., and C. D. Michener. 1987. Tribes of Xylocopinae and origin of Apidae. Annals of the Entomological Society of America 80: 439-450.

Schenck, A. 1859. Beschreibung Nassauischer Bienenarten. Jahrbucher des Vereins für Naturkunde im Herzogthum Nassau 14: 1-414.

Schenck, A. 1869. Beschreibung Nassauischen Bienen, Zweiter Nachtrag. Jahrbucher Nassau des Vereins für Naturkunde 21-22: 269-382.

Schmiedeknecht, O. 1882. Apidae Europaeae. Vol. 1, xiii + 383 pp. Berlin.

Schönitzer, K. 1986. Comparative morphology of the antenna cleaner in bees. Zeitschrift für Zoologische Systematik und Evolutionsforschung 24: 35-51.

Schönitzer, K., and M. Renner. 1980. Morphologie der Antennenputzapparate bei Apoidea. Apidologie 11: 113-130.

Sheppard, W. S. and B. A. McPherson. 1991. Ribosomal DNA diversity in Apidae. Pp. 87-102 *in* D. R. Smith (ed.), Diversity in the Genus *Apis*. Boulder, Colorado: Westview Press.

Silveira, F. A. 1993. Phylogenetic relationships of Exomalopsini and Ancylini. University of Kansas Science Bulletin 55: 163-173.

Silveira, F. A. In press. The mouthparts of *Ancyla* and the reduction of the labiomaxillary complex among long-tongued bees. Entomologica Scandinavica.

Smith, F. 1853. Catalogue of Hymenopterous Insects in the Collection of the British Museum, Part 1, [i] + 1 + 197 pp., 6 pls. London.

Snelling, R. R., and R. W. Brooks. 1985. A review of the genera of cleptoparasitic bees of the tribe Ericrocini. Contributions in Science, Natural History Museum of Los Angeles County, no. 369: 1-34.

Snodgrass, R. E. 1956. Anatomy of the Honey Bee. Ithaca, New York: Cornell University Press. i-xiv + 1-334 pp.

Šustera, O. 1958. Übersicht des Systems der paläarktischen und mitteleuropäischen Gattungen der Superfamilie Apoidea. Acta Entomologica Musei Nationalis Prague 32: 443-463.

Swofford, D. L. 1990. Phenetic Analysis Using Parsimony, Version 3.0g. Champaign, Illinois: Illinois Natural History Survey.

Tkalců, B. 1972, 1974. Arguments contre l'interprétation traditionnelle de la phylogénie des abeilles. Bulletin de la Société Entomologique de Mulhouse, Apr.-June 1972: 17-28; Apr.-June 1974: 17-40.

Thomson, C. G. 1872. Skandenaviens Hymenoptera, vol. 2, pp. 1-286. Lund.

Warncke, K. 1977. Ideen zum natürlichen System der Bienen. Mitteilungen Münchner Entomologischen Gesellschaft 67: 39-63.

Warncke, K. 1979. Beiträge zur Bienenfauna des Iran: 10. Die Gattung *Ancyla* Lep., mit einer Revision der Bienengattung *Ancyla* Lep. Bollettino del Museo Civico di Storia Naturale di Venezia 30: 183-195.

Whitfield, J. B. 1992. Phylogeny of the non-aculeate Apocrita and the evolution of parasitism in the Hymenoptera. Journal of Hymenoptera Research 1: 3-14.

Winston, M. L. 1979. The proboscis of the long-tongued bees: A comparative study. University of Kansas Science Bulletin 51: 631-667.

Zeuner, F. E., and F. J. Manning. 1976. A monograph on fossil bees. Bulletin of the British Museum (Natural History), Geology 27: 149-268, pls. 1-4.